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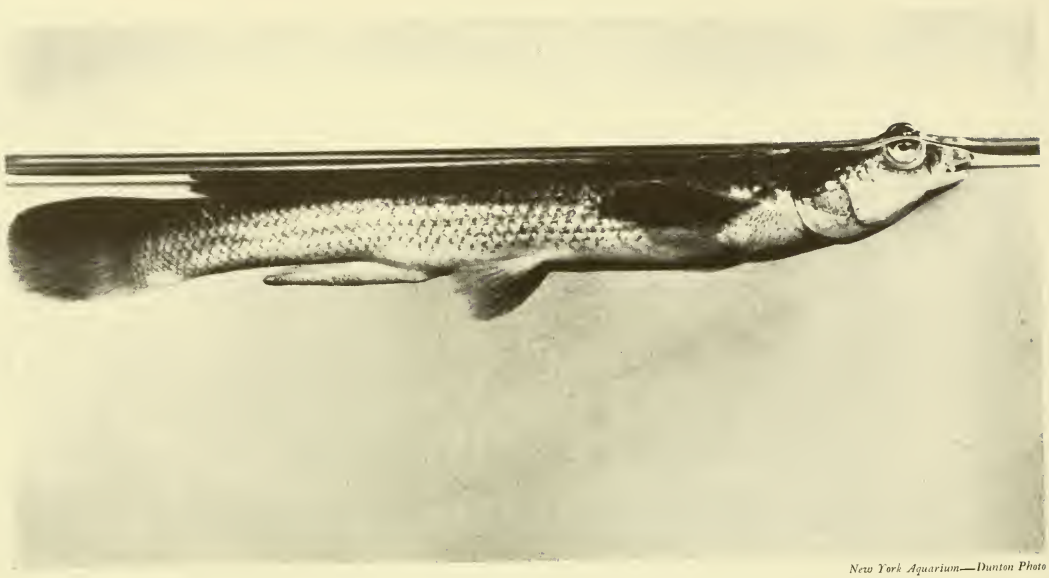

New York Aquarium—Dunton Photo

THE 'FOUR-EYED FISH', *ANABLEPS ANABLEPS*, CRUISING AT THE SURFACE WITH THE AËRIAL PUPIL ABOVE WATER LEVEL AND THE AQUATIC PUPIL IMMERSED.

(*See p. 434*)

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THE VERTEBRATE EYE
AND ITS ADAPTIVE RADIATION

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HAFNER PUBLISHING COMPANY
New York London
1963

reprinted by arrangement with
The Cranbrook Institute of Science

Printed and Published by
Hafner Publishing Company
31 East 10th Street
New York 3, New York

Library of Congress Catalog Card Number 63-17545

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The Cranbrook Institute of Science
Bloomfield Hills, Michigan

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PREFACE

The structural patterns of vertebrate eyes have been undergoing intelligent scrutiny for about a century and a half. In that time, and more and more rapidly toward the present, men have been learning much about the functional meanings of those patterns, and their rôles in the lives of the animals which have produced them. It has seemed to me that it is time an attempt was made to interpret comparative ocular biology as a whole to those who want to know what the eye is all about, but are repelled by the pedantic terminology of anatomy texts, the mathematics of physiological optics, the scatteredness of the ecological literature, and the German language. In this book, I have made such an attempt.

I have chosen the term 'adaptive radiation' for the subtitle of this work deliberately. It was coined by Henry Fairfield Osborn to describe the manner in which animal groups have become diversified in pouring themselves into a number of environmental molds which were made available to them more or less simultaneously. It is a little unusual to speak of the adaptive radiation of an *organ;* but I can think of no better way to express what the vertebrate eye has done in modifying its pattern to fit itself for the many different kinds of performance demanded of it by its adaptively-radiated owners.

The investigation of anatomy for its own sake is pretty well defunct. The study of structures in relation to their employment by the animal has hardly begun. When I started writing this book, I had never heard of the late Hans Böker; but, in discussing the eyes of vertebrates in terms of adaptation to environment, I believe I have followed the principles of his 'comparative *biological* anatomy', which have so revivified the study of anatomy in recent years.

If the comparative ophthalmologists of the world should ever hold a convention, the first resolution they would pass would say: "Everything in the vertebrate eye means something." Except for the brain, there is no other organ in the body of which that can be said. It does not matter in the least whether a liver has three lobes or four, or whether the tip of the heart points north or south, or whether a hand has five fingers or six, or whether a kidney is long and narrow or short and wide. But if we should make comparable changes in the makeup of

a vertebrate eye, we should quite destroy its usefulness. Man can make optical instruments only from such materials as brass and glass. Nature has succeeded with only such things as leather and water and jelly; but the resulting instrument is so delicately balanced that it will tolerate no tampering.

And yet, vertebrate eyes are not all alike—far from it. Each is a cluster of harmonious parts, and the changes which have converted one type of eye into another, through evolution, have necessarily involved most of its parts. When one feature has had to be altered for some primary ecological reason, this alteration has in turn called for concurrent secondary alterations of other structures, with the whole complex remaining harmonious and workable at all times. Of course, many eyes contain little odds and ends of structures which have no function. But in every such case, one can be sure that the structure in question did not arise in its present form, but is a vestige of a once important part which is no longer needed, or whose task has come to be done better by something else in the eye. When such remnants are in the way—and they usually are—the eye gets rid of them promptly, which may add greatly to the difficulty of determining how the ocular pattern of a given group was ever derived from that of a known ancestor. Fortunately, however, there are few such gaps; and it is now possible to tell a well-connected story of the evolution of almost any particular vertebrate eye.

This book will be of particular benefit to zoölogists and ecologists, medical and veterinary ophthalmologists, and comparative psychologists. But since none of these people speak the others' languages, I have been able to assume no more scientific knowledge on the reader's part than the contents of the usual elementary course in biology. The book should therefore be entirely clear to any college student or graduate, and to any amateur naturalist—'trained' or not. As each unusual term has been introduced, I have either defined it there and then or else placed it in the glossary. The reader will find that the difficulty of the reading fluctuates, which is inevitable in view of the varying weightiness of the material. Some things about the eye and its workings are intricate, but I must disclaim all responsibility for that—there are some subjects, such as astrophysics and thermodynamics, which no writer could possibly 'popularize'. The reader will also soon note that my mode of expression is strongly tainted with teleology. I do not expect this to mislead anyone—it is merely an economy device, for it saves many words to say simply that an animal has produced this feature or that to fill such-and-such a need.

The material of the book is progressive, though this may not seem to be indicated by the table of contents. I could not explain everything at once, but I have so arranged matters that a given discussion will be perfectly lucid if the reader has not skipped much before it. I hope, naïvely of course, that anyone who reads in the book at all will read the whole of it. It is not designed as a reference book, in which to 'look up' small points from time to time. Rather, it has been written in the style of a text-book, though for a course which has yet to be given in any American university. The book is not documented, *i.e.* loaded up with specific citations for every point of fact and reasoning which has originated outside of my own studies. The average reader will not miss them; and the earnest student who reads the book, and is led thereby to want to do research in its field, will have to devour all of the required reading listed in the bibliography anyway. He—and the established investigator in the field—will readily know which of my pronouncements to blame upon me alone. If not, he is free to write to me for specific bibliographic assistance, which I shall gladly furnish within the limitations of my time and ability.

Part I has been called 'basic' because it incorporates the first bodies of information which the reader should have if he knows little or nothing about the eye to begin with—even if he intends to skip straight to Chapter 17 to find out what the pecten means. It is strongly urged that every reader, even the ophthalmologist, read all of Part I before attempting to appreciate other chapters. In it, the human eye and human vision have been used to acquaint the reader thoroughly with one sample eye and its workings. The all-important retina is discussed in general terms. The origins of the eye, ontogenetic and phylogenetic, are explained; and the elementary facts of vertebrate inter-relationships are set forth so that the non-zoölogical reader will understand the necessary taxonomic allusions in Part II and the discussions of relationships and derivations in Part III.

Part II is the ecological body of the work. Here are gathered together, under the banners of various environmental factors, the evolutionary responses of the vertebrate eye to those factors. In these chapters, at some risk of cluttering, I have included many cross-references to ensure that the reader who insists on dabbling will not miss information pertinent to the satisfaction of his momentary curiosity. Some matters are expounded in more detail than others, somewhat in proportion to the interest I have found them to arouse—the subject of animal color

vision, for example, is treated at particular length because no questions are so often asked of the comparative ophthalmologist as those under this aegis. Part II is an exposition of fundamental ideas rather than a compendium of both explicable and at-present-useless facts. Because of its ecological viewpoint, whole great fields find no place in it (or elsewhere in this book)—ocular biochemistry, retinal photo-electrics, clinical veterinary ophthalmology, most of physiological optics, and so on. These chapters are intended to stimulate as well as to inform, and both here and in Part III there is emphasis upon the more conspicuous of the unsolved problems which await new students.

Part III traces the history of the eye, group by group, from the lowest living vertebrates to the highest. Here, place has been made for those features which are of importance to the eye itself as a living thing, but are not discernibly concerned in its performance in relation to the special environment of its owner. The emphasis in these synoptic chapters is on the morphology of the eye, the evolution of that morphology, and the bearing of it upon the problems of vertebrate phylogeny. The animal as a whole explains much about its eye, and in turn the eye can often explain much about the animal. Thus, the structural plan of the snake eye, its possible mode of origin, and the significance of this for the evolutionary history of the snakes, are all interconnected matters. The reader will find numerous sub-indices in Part III which will enable him to round up quickly all the information about his favorite group which has been given earlier in the book, and is omitted here to avoid duplication and waste of space.

The illustrations have been kept as simple as possible, considering the intricacies of the subject. Many are original, several of them—quite beyond my ability to make—beautifully drawn by the Misses Sylvia Hagyard and Gladys Larsen. Many others have been borrowed photographically from the journals, with or without changes (which are noted in the legends), and relabelled in accordance with a uniform scheme. Here, much of the burden of work fell upon Albert Schlorff, without whose expert photographic assistance I should have been quite helpless. I must also acknowledge with gratitude the kindness of Viktor Franz in permitting the free use of illustrations from his work. Figures 4, 5, and 41d are by courtesy of William Bloom and the W. B. Saunders Company, publishers of his 'Maximow's Text-Book of Histology'. Figures 6a and 16 are modified from Adler's 'Clinical Physiology of the Eye', by permission of The MacMillan Company, publishers.

A great number of my friends have helped materially to make this book possible, by criticizing portions of the manuscript relating to their specialties, by furnishing specimens, information, or technical assistance; and in other ways. I could not omit to mention some of them by name: Ermine C. Case, Alfred Cowan, Elizabeth Crosby, Brian Curtis, Walter F. Grether, Parker Heath, Selig Hecht, Arlington C. Krause, George E. Lathrop, Wade H. Marshall, George A. Moore, Kevin J. O'Day, Erich Sachs, John F. Shepard, Alec Skolnick, Gabriel Steiner, Francis B. Sumner, Samuel A. Talbot, and Burton D. Thuma. During the writing, generous financial support was forthcoming from the Wayne University College of Medicine and from the Jennie Grogan Mendelson Memorial Fund for Ophthalmology. During the actual making of the book, the expert and sympathetic guidance of William L. Wood, director of the Cranbrook Press, has been invaluable.

I am particularly obligated to the curators of the Museum of Zoölogy of the University of Michigan and the Cranbrook Institute of Science who read the entire text and straightened my kinks in their especial realms: Carl L. Hubbs (fishes), Helen T. Gaige (amphibians and reptiles), Josselyn Van Tyne (birds), and Robert T. Hatt (mammals).

Finally, I am most deeply indebted of all to Director Hatt and the Trustees of the Institute for their invitation to write the book as one of their series of Bulletins, and for their generosity in the allowance of space and illustrations. As is so usual with such books, the problem has been to know how much to leave out. My trepidations in this connection have led, during the writing, to several upward revisions of the expected size of the work. I have felt as though I were behaving rather like the camel which at first asked only to warm his nose within the Arab's tent, and finished by crowding out the owner. My conscience will be easier if most of my readers are glad that the book was not smaller.

G. L. W.

Detroit, Michigan
May, 1942

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Part I — Basic

Chapter 1

LIGHT AND ITS PERCEPTION

The principal means by which most animals are made aware of their surroundings, and changes in these surroundings, is the reflection or emission of light toward them by external objects and the reception of this light by special organs which we term photoreceptors. The more complicated of these photoreceptors are called eyes, though it is not complexity, as such, which governs the applicability of that special term. We say that the function of the eye is vision, but since all photoreception is not vision and not all photoreceptors are eyes, we must consider these broader and narrower terms before delving into our subject proper—the structure and variations of vertebrate eyes and their relation to the ways of life of their possessors.

Light may best be defined, for our purposes here, as a rhythmic emanation of energy whose rhythm-frequency or pitch falls within definite limits, outside of which are the higher or lower frequencies of radio, cosmic, X-, and other rays. Visible light thus forms a circumscribed band of frequencies to which the eye happens to be sensitive and which, compared with all forms of radiant energy in general, is like a single octave toward the high-pitched end of the scale of a piano (see Table I). It contains only a small fraction of the total amount of energy given off by the sun, and sunlight in turn forms only a portion of the 'grand spectrum' of radiant energy. Like other forms of radiant energy, light in its ultimate units can vary in but simple ways—in speed, in frequency, and in intensity. But natural lights and illuminations are complex mixtures of these variations, and make possible the infinite variety of nature's pictures, varying in tone or shading (owing to combinations of intensities) and in color or hue (owing to combinations of frequencies).

We have been discussing light as an objective physical entity; but, just as there would be no sound if a tree were to fall with no one to hear it, so also there would be no light in the physiological sense if there were no photoreceptor upon which it impinged. In this other sense light is a sensation, an experience in consciousness. Like other such experiences, it may be evoked by a limited number of causes (other than actual

physical light). The qualities of a light-sensation bear only a close, not an absolute, relationship to the objective attributes of a physical light which produces it. Thus, different colors may be seen under special circumstances when the corresponding different frequencies of light are not being steadily presented to the eye at all, or the same color may result from totally different mixtures of frequencies. Two lights with the same energy-content may appear different in brightness while two others, equally bright, may differ greatly in actual physical intensity. Color and brightness are thus subjective correlates of the objective frequency and intensity. The former can be perceived but not measured, while the latter can be measured with inanimate instruments but cannot be perceived with the eye.

A sobering array of optical illusions may be seen by the reader in any good reference work on psychology, and will serve to teach, still more emphatically, the lesson that: "Our eyes do not see; but we see with our eyes." Photoreception is one thing—it may be conscious, the reception of the external stimulus of light upon the sill of the "window of the soul"—or it may lead reflexly to quite unconscious activities such as the change of the size of the pupil, the aiming of the eyes, the blinking of the lids when the eye is about to be struck by something, and so on.

Vision is something more. It is the complex and sometimes deceptive product of the interaction of the simple information which travels along the optic nerve and the manipulations, as yet unfathomable, which this information undergoes in the brain before it is presented to the consciousness for action or other disposal.

A photoreceptor may be constituted by a single part of a one-celled animal; by one of a number of similar, scattered, photosensory cells in an invertebrate's skin; by a patch of cells closely aggregated into a plate, or lining a pit; or by an ocellus or eye (Fig. 1). This last term is best reserved for those photoreceptors in which there is a light-sensitive layer of cells upon which accessory parts converge the light rays received from environmental objects. An eye, then, ordinarily contains at least a photosensory epithelium or retina, and a lens. An image may however be formed upon the retina by a pinhole (as in the chambered nautilus) instead of by a lens; or, the lens in a given type of eye may be employed to concentrate the light in order that the eye may work in dimmer illuminations, instead of to form an image so that the mind may have a picture. Finally, a number of 'concentrator' units may be congregated so that a mosaic image can be built up in the consciousness itself, and it is upon

this plan that the 'compound' eyes of many arthropods are constructed.

Vertebrate eyes are all built upon one fundamental plan. With the exception of those which have degenerated because their owners live underground, or in the perpetual night of caves or the depths of the ocean, they are provided with a retina and with a lens whose optical properties are such that it forms an image upon the retina. The lenses of the median eyes which some reptiles possess on the top of the head are probably often of the concentrator type; but those of the lateral, or ordinary, eyes are nearly always eikonogenic—that is, image-forming.

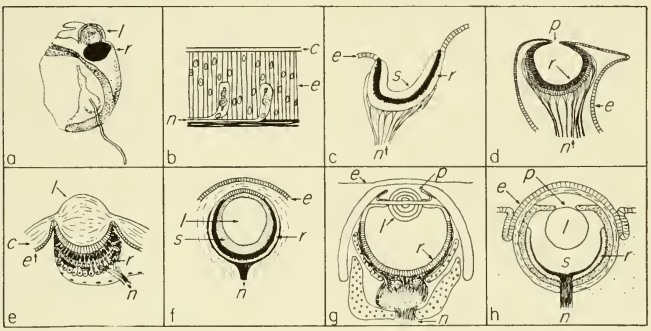

Fig. 1—Various photoreceptors.

a, intracellular type in a one-celled animal, *Pouchetia cornuta*. b, scattered photosensory cells in the skin of an earthworm. c, pit-like visual organ of a limpet, *Patella*. d, pinhole-camera type of eye in the chambered nautilus. e, ocellus of a scorpion, *Euscorpius*, with concentrating lens. f, eye of a snail, *Murex*. g, image-forming eye of a squid, *Loligo*. h, eye of vertebrate.

c- cuticle; *e*- epithelium; *l*- lens; *n*- nerve fibers; *p*- pupil; *r*- retina; *s*- secreted material.

Before we pass to a consideration of the detailed structure and workings of a standard vertebrate eye, it needs to be further emphasized that vision, *seeing*, is a phenomenon of the mind plus the eye and not of the eye alone. It would probably not stagger any reader of this book to be asked to believe that a worm may react to a light-stimulus without having a sensation or consciousness of light. Vertebrate vision as we ourselves experience it, however, is more than just photoreception. Vertebrate visual mechanisms, from fish to mammal, are so nicely constructed that so far as the eyes themselves are concerned, they may in many cases send

TABLE I — THE GRAND SPECTRUM OF ELECTROMAGNETIC RADIATION

Kind of Radiation:			Usual Source:	Wavelength Ranges and Units: X units (X) 1000 = 1	Ångström units (Å.u.) 10 = 1	Millimicrons (mμ) 1000 = 1	Microns (μ) 1000 = 1	Millimeters (mm.) 1000 = 1	Meters (m) 1000 = 1	Kilometers (Km)	Octaves:
Slow electromagnetic			Coil rotating in a magnetic field							> 30	?
Hertzian (Radio)			Spark discharge, oscillating triode				100----------to----------30				35.5
LIGHT	Infra-red (Heat)		Hot bodies			760---to----?					
	Visible Spectrum	Red	Hot bodies (above 500°C) and ionized gases			< 760					1
		Orange				center at 600					
		Yellow				" " 582					
		Green				" " 515					
		Blue				" " 476					
		Indigo				424 to 455					
		Violet				> 390					
	Ultra-violet	Long			3000-3900						21
		Short			1850-3000						
		Extreme			< 100-1850						
Röntgen ("X") rays			Sudden arrest of swift electrons	< 10---to--> 150							
Gamma (of radio-active substances)			Disintegrating atomic nuclei	< 1-1400							
Cosmic (electro-mag. component)			Not surely known	.002-0.1							

to the central nervous system all of the information that human brains receive from human eyes. That does not mean at all, however, that the same use and value is ever made and obtained from that information.

Many vertebrates with perfectly good eyes, as complex as our own, may not see anything. In explanation of this perhaps surprising statement, it may be enough to point out that the portion of the brain in which human visual impulses terminate and are integrated—in which, in other words, vision seems to reside—is not present in the brains of fishes at all. A fish may have a knowing look in his eye as he passes up one kind of fly and avidly seizes another, but we have no right whatever to assume that he sees either fly, or indeed anything else. It is quite possible that he is acting, like the worm, only reflexly and without conscious accompaniments to patterns of shade and hue which, given a brain capable of the analysis ours can perform, would be mental pictures to him as they are to us.

When therefore, elsewhere in this book, such questions are raised as: "Do dogs see colors?" and "Can fishes tell a square from a triangle?" the reader must visualize 'see' and 'tell' in tell-tale quotation marks, and bear with the writer if he seems to lapse into anthropocentrism and to attribute conscious visual acts to animals whose dim minds we cannot read. It is easiest to compare the visual potentialities of one ocular mechanism with those of another *as though* behind each there lay a brain like that of man; but it is hoped that without further frequent reminder, the reader will forever remember this:

Human vision, so valuable and so kaleidoscopic, is the product of a complex brain teamed with a relatively simple eye; and when we sometimes encounter more complex eyes (which are *always* connected with simpler brains) we must not assume that they afford their owners anything so informative of the environment as does the vision we experience. "Nothing is in the mind which is not first in the senses"—but the sense-organs, and particularly the eye, may offer the mind much more than the latter can assimilate.

Chapter 2

A TYPICAL VERTEBRATE EYE: THE HUMAN

(A) Structures and their Functions

The human eye will serve admirably as an introduction to vertebrate ocular morphology and physiology, for it is fairly well generalized and presents no bizarre features. In the ensuing discussion, fine structural and terminological details will be given only where they are important for an understanding of the workings of the eye. Any detailed descrip-

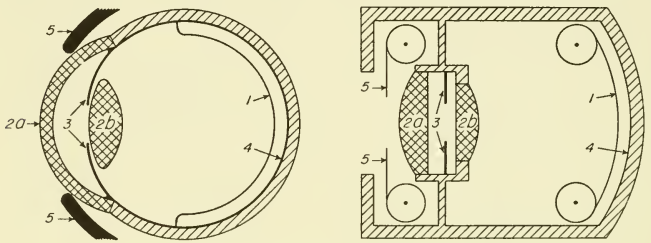

Fig. 2—Comparison of eye and camera.

Parts which correspond in function bear similar numbers. *1*- retina = film, on curved track; *2a*- cornea = front element of lens; *2b*- crystalline lens = rear element of lens; *3*- iris = diaphragm between lens elements; *4*- pigment of chorioid coat = flat black paint; *5*- eyelids = roller-blind shutter.

tion of the human retina will be omitted here, since a general treatment of the vertebrate retina is given in Chapter 3. The reader who wishes to learn the histology of the human eye for its own sake will of course study actual preparations and a textbook of microscopic anatomy.

The Eye a 'Camera'—It is almost a cliché to say that the eye is built like a camera (Fig. 2). In each there is a sensitive screen (retina = film or plate) on which an inverted image is formed by a lens (cornea + crystalline lens = lens). One device (lids = shutter) can exclude light, which when admitted by it is regulated in amount by a variable aperture (pupil = diaphragm aperture). The interior is darkened (chorioid pigment = dead black paint) so that internal reflections will not blur or

multiply the image. Lastly, the whole apparatus can be set to take equally sharp pictures at different distances (accommodation = substituting one lens for another in the camera, or varying distance between lens and film).

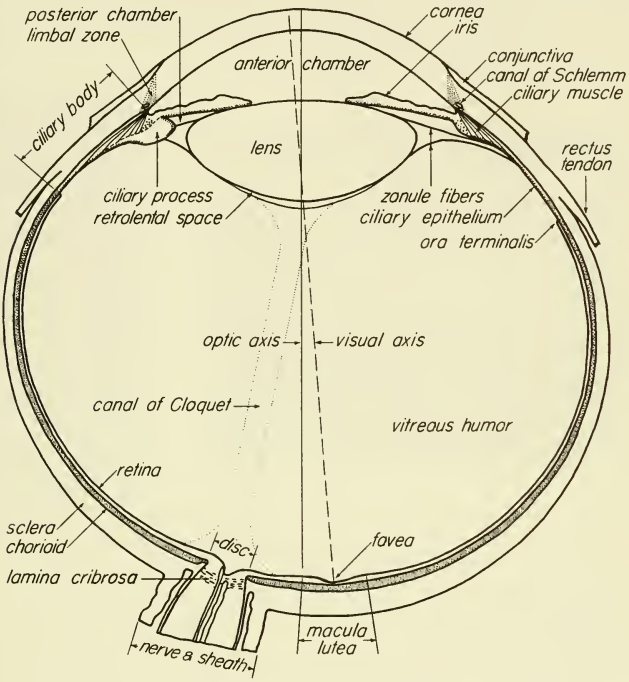

Fig. 3—Horizontal section of right human eye. × 4. Modified from Salzmann.

On the left, the section contains a ciliary process behind which the zonule fibers are partly concealed; on the right, the section has passed between two ciliary processes and the full extent of the zonule fibers can be seen. The limbal zone (transition between cornea and sclera) is stippled to emphasize that it is broader internally than externally.

The Fibrous Tunic—The outer case of the living camera is formed by the fibrous tunic, consisting of the sclera and the cornea, the latter seemingly a transparent anterior continuation of the sclerotic coat which

is more sharply curved than the latter (Fig. 3). A substantial portion of the thickness of the cornea represents the skin of the head, which during evolution became affixed to the eyeball, leaving loose places, to permit eye movements, up underneath the eyelids where it merges with their linings to join the ordinary outer skin at the lid margins. Only some of the inner layers of tissue in the cornea represent a clear window in the original, ancestral, fibrous capsule. As a matter of fact, the sclera itself

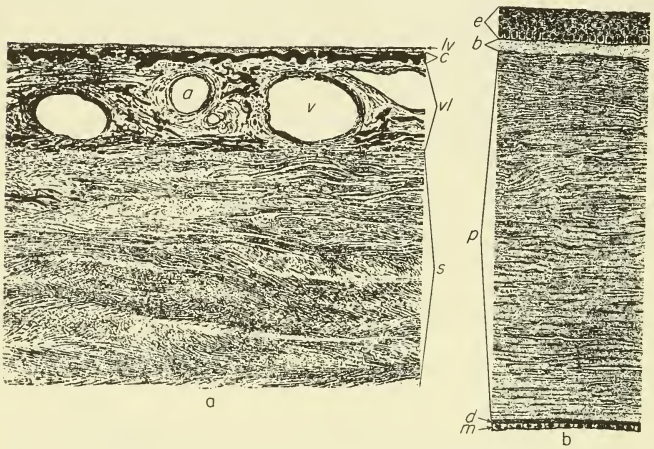

Fig. 4—Fibrous and vascular tunics of the human eyeball. × 135.
Modified from Maximow and Bloom, after Schaffer.

a, sclera and chorioid.

a- artery; *c*- choriocapillaris layer of chorioid; *lv*- lamina vitrea; *s*- sclera; *v*- vein; *vl*- vascular, pigmented layers of chorioid.

b, cornea.

b- Bowman's membrane; *d*- Descemet's membrane; *e*- epithelium; *m*- mesothelium; *p*- substantia propria.

is almost as transparent as the cornea in many of the lower vertebrates. The 'white' of the human eye is differentiated from the clear cornea not because the latter has become transparent secondarily, but rather because the sclera has become clouded. What has happened in evolution also takes place in individual development, and the clear parts of the embryonic eye are clear from the start and remain so—they do not *become*

so. Despite this easily ascertained fact, many speculations have been made as to what factor is responsible for the transparency of the cornea and the lens. The really interesting question is, what makes the other tissues of the developing embryo become opaque.

The sclera (Fig. 4a, *s*) is composed of tough, inelastic, tendinous tissue organized in ribbon-like bundles of microscopic fibers which are felted together in such a way that the whole tissue is about equally strong in all directions—to resist the intraocular pressure, equal of course in all directions, without allowing the eyeball to change its shape. The flat fiber-bundles are of unknown length, for their ends cannot be found; but each seems to arise somewhere behind the rim of the cornea, runs parallel thereto for a space, then courses backward around the eye and forward again in a wide loop—not, however, following a great circle of the ocular sphere. The tissue of the sclera contains very few cells. It consists chiefly of the lifeless fibers, and its rate of living (metabolism) is so low that it requires no direct blood supply. Nearly all of the blood vessels to be seen in sections of the sclera are merely passing through it on their way into or out of the chorioid coat.

The layers of fibers in the cornea (Fig. 4b) are not so much felted as in the sclera, but run more nearly parallel with less interchange of fibers between layers. The cells between them are consequently more definitely organized into layers also; but they are scattered very far apart in a given layer. The substance of the healthy cornea is quite devoid of blood vessels, which would interfere with transparency. At the same time, it is so firm that the diffusion of liquids through it is much impeded. Its living cells, the corneal corpuscles, therefore join hands by means of long, delicate threads of living protoplasm along which nutriments and wastes may be transported to and from the blood vessels surrounding the margin of the cornea. The avascularity of the cornea, and evaporation from its surface, make it several degrees cooler than the body as a whole, and the metabolism of the corneal cells is adjusted to the lower temperature.

The change in the character of the tissue, as one passes from the sclera into the cornea, is a gradual one and the wide region of transition noted marks the limbus (rim) of the cornea. A flange of scleral substance, the scleral roll, (Fig. 5, *sr*) overlaps the edge of the cornea on its inner surface so that the illusion of the cornea being set in the sclera, like a watch-crystal in its bezel, is created. The two portions of the fibrous tunic are not actually at all easily separable, but the limbus is the weakest region

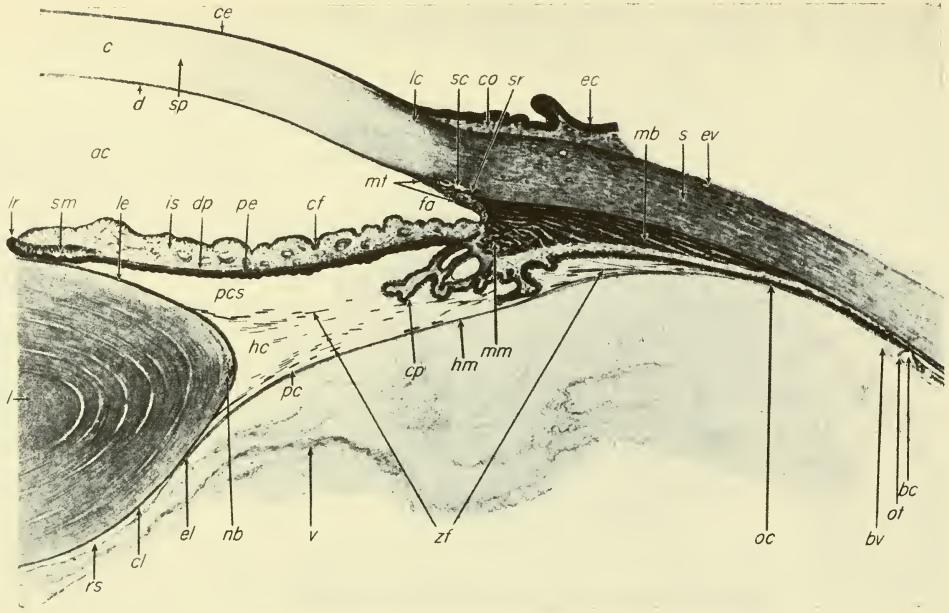

Fig. 5—Structures of the anterior segment of the human eye. ×17. From Maximow and Bloom, after Schaffer.

ac- anterior chamber; *bc*- Blessig cyst; *bv*- base of vitreous (zone of firm attachment to ciliary epithelium); *c*- cornea; *ce*- corneal epithelium; *cf*- contraction furrow; *cl*- capsule of lens; *co*- conjunctiva; *cp*- ciliary process (chopped up by sectioning knife); *d*- Descemet's mesothelium and membrane; *dp*- dilatator of pupil; *ec*- epidermis of conjunctiva; *el*- Egger's line (zone of fusion of hyaloid membrane of vitreous to lens capsule); *ev*- episcleral vessel; *fa*- filtration angle; *hc*- Hannover's 'canal'; *hm*- hyaloid membrane of vitreous; *is*- iris stroma; *l*- lens; *lc*- limbus of cornea; *le*- lens epithelium; *lr*- limit of retina at pupil margin; *mb*- muscle of Brücke (meridional, radial fibers of ciliary muscle); *mm*- muscle of Müller (circumferential fibers of ciliary muscle); *mt*- meshwork tissue separating Schlemm's canal from anterior chamber; *nb*- nuclear bow in lens epithelium, at site of conversion into lens fibers; *oc*- orbiculus ciliaris; *ot*- ora terminalis of sensory portion of retina; *pc*- Petit's 'canal'; *pcs*- posterior chamber (in strict sense); *pe*- pigment epithelium of iris (posteriormost of two layers of retinal cells); *rs*- retrolental space (communicates with canal of Cloquet, not shown); *s*- sclera; *sc*- Schlemm's canal; *sm*- sphincter muscle; *sp*- substantia propria; *sr*- scleral roll (narrow shelf of scleral tissue, on under side of which ciliary muscle fibers take their origin); *v*- vitreous; *zf*- zonule fibers.

in the fibrous tunic. It is at the limbus that an isolated eyeball will rupture, if it is squeezed until it bursts.

The outer surface of the fibrous mass (substantia propria) of the cornea is covered by a stratified epithelium which is much like that lining the mouth, and lacks the dead, horny outer layers which are present on the general epidermis of the body. This corneal epithelium (Fig. 4b, *e*; Fig. 5, *ce*) is continuous, at the limbus, with the thicker and less regular epithelium of the conjunctiva (Fig. 5, *ec*). The conjunctiva (Fig. 5, *co*) represents head skin which at the margins of the upper and lower eyelids is doubled back on itself up underneath them to form their linings, and is continuous over the front of the eyeball, with which it is fused to form the 'conjunctiva fixa'—the loose folds in the culs-de-sac up under the lids being the 'conjunctiva libera'. The connective-tissue dermis of the conjunctiva fixa can hardly be distinguished from the loose connective tissue which clings to the sclera; but at any rate it stops at the limbus and only the epidermis appears to continue over the cornea.

Actually the dermis belonging to the corneal-epithelium part of the conjunctiva is represented by some of the outermost layers of the substantia propria—no one can say just how many, in the case of the human eye. The very outermost layer, just beneath the epithelium, is devoid of cells and stains a little differently. It is known as Bowman's membrane (Fig. 4b, *b*); but it scarcely deserves recognition and in the lower animals cannot ordinarily be made out at all as a distinct part of the substantia propria.

The corneal epithelium is richly supplied with pain-sensory nerve endings and apparently with no others, and is remarkable for the speed with which it can grow to repair or replace itself if injured. There is some reason to think that it is normally nourished from entirely outside the body—from the tears, which contain appreciable amounts of nutrient substances.

The inner surface of the cornea is lined by a thin pavement of cells usually called the endothelium of the cornea. (It more properly deserves to be considered a portion of the mesothelium of the anterior chamber, however, since it is continuous with the anterior covering of the iris and the term 'endothelium' is outmoded as applying to mesodermal epithelia generally). Between the substantia propria and the mesothelium, and secreted by the latter as its basement membrane, is the thin, homogeneous, elastic 'membrane of Descemet' (Fig. 4b, *d*).

It needs to be made clear at this point that the adjective 'elastic', wherever it is applied to an ocular structure, means 'springy' rather than 'easily stretched'—thus Descemet's membrane, the lens capsule, the zonule fibers and so forth are elastic in the sense of a celluloid strip, not of a rubber cord.

The Intra-Ocular Fluids—The fibrous tunic is normally kept distended to the point of rigidity by the pressure of fluid secreted within the eye. This fluid, the aqueous humor, is continuously produced at a slow rate and drained out of the eyeball into the blood stream by a complex arrangement which is so regulated that the intra-ocular pressure remains roughly constant at about 25 millimeters of mercury. Half of this internal pressure is created by the external pressure of the extra-ocular muscles and if both these and the blood-vessels leading to the eye are severed, the intra-ocular pressure falls to about 10 millimeters of mercury. Overproduction of aqueous humor or any chemical, mechanical, or pathological upset in the drainage system will lead to a painful rise in pressure, the condition being known as glaucoma. If the pressure is unrelieved, it clouds the cornea and injures the retina, and the end result is blindness.

The greater portion of the intra-ocular fluid, occupying the large chamber in the back of the eye, is rendered gelatinous by the addition to it of proteins secreted during development by the retina. This mass of gelated aqueous is called the vitreous (= glassy) body, or vitreous humor (Fig. 3; Fig. 5, *v*). It is relatively permanent and in the fully grown eye it is fixed in amount, so that any portion of it which is lost through a wound is replaced only by watery aqueous humor. It is mostly to the unmodified aqueous, in the front of the eye, that fresh fluid is constantly added; and it is with the liquid aqueous that the pressure-regulatory drainage mechanism—the canal of Schlemm (Fig. 3; Fig 5, *sc*) communicates in an indirect way.

So far as the human eye itself is concerned, there is no powerful reason why the material which fills the chambers of the eye should be of two kinds—liquid anteriorly and semi-solid posteriorly. But in the forebears of the fishes, which invented the vertebrate eye, the material near the cornea had to be kept fluid so that the lens could be readily moved in accommodating the focus of the eye to different distances, and the lens would have dropped back into the globe if there were only liquid behind it. In the higher vertebrates, the lens is not changed

in position but only slightly altered in shape, and it is held firmly in place by ligaments which the lower fishes lacked; but the differentiation in consistency of the intra-ocular media has never been abandoned. This is probably fortunate, as otherwise, in animals above the fishes, the evolution of a muscular iris and mobile pupil might have been inhibited.

The Uveal Tract—The layer of the eyeball wall next inside the fibrous tunic, clinging closely to the sclera but swinging inward away from it at the sclero-corneal junction, is the uveal tract or uvea. The part of the uvea which is attached to the sclera is a thin, deeply pigmented layer consisting mostly of blood vessels, with connective tissue binding them into a membrane. It is called the chorioid coat (Fig. 3; Fig. 4a). The pigmentation of the chorioid prevents internal reflections and keeps light from getting through the wall of the eyeball indiscriminately, and the rich vascularity of the tissue is concerned with the nutrition of the highly metabolic retina.

Against the inner surface of the uveal tract, throughout its extent, lies the retina (Fig. 3). Where it is in contact with the chorioid, the retina is thick (pars optica) and is sensitive to light. The anterior portions of the uveal tract are lined with a thin, insensitive continuation of the retina (pars cæca), which thus really terminates at the rim of the pupillary aperture.

The sensory part of the retina has the form of a cup whose lip, the 'ora terminalis' (Fig. 3; Fig. 5, *ot*), is an important landmark inside the eyeball. From the ora forward, both retina and uvea are profoundly modified. The chorioid, at that point, thickens and ceases to be so heavily pigmented and vascularized. The thickened region forms, in a sagittal section, a slender triangle with its narrow angle aimed posteriorly to merge into the chorioid. This thickened zone of the uvea is called the ciliary body (Figs. 3 and 5), and it is characterized by the presence of many involuntary muscle fibers and, on its inner surface anteriorly, a large number (70-80) of radially arranged fin-like structures, the ciliary processes. Each ciliary process (Fig. 3; Fig. 6c; Fig. 7g) is essentially a fold of non-sensory retina covering both sides of a flat sheet of small blood vessels. Retina and uvea thus intimately coöperate to form the ciliary processes. The anterior part of the ciliary body which bears them is termed the corona ciliaris. At the posterior ends of the processes they diminish in height and fade down to the level of the valleys between them. This leaves, between the hind ends of the processes

and the ora terminalis, a fairly smooth posterior region in the ciliary body, called the orbiculus ciliaris (Fig. 3; Fig. 5, *oc*; Figs. 6c, 7g, *cor, orb*).

Inasmuch as it is from the blind epithelial part of the retina covering the ciliary body that the aqueous humor is given off, the ciliary processes and the less conspicuous secondary folds between them are best interpreted as a device for greatly increasing the secretory surface for the

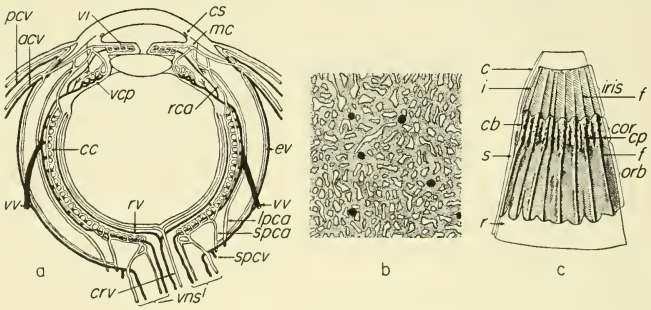

Fig. 6—Vascular structures of the human eye.

a, vascular plan of the eye, showing veins in black, arteries clear. Modified from Adler, after Leber.

acv- anterior ciliary vessels; *cc*- choriocapillaris; *crv*- central retinal vessels; *cs*- canal of Schlemm; *ev*- episcleral vessels; *lpca*- long posterior ciliary artery; *mc*- major circle of iris; *pcv*- posterior conjunctival vessels; *rca*- recurrent chorioidal artery; *rv*- retinal vessels; *spca*- short posterior ciliary artery; *spcv*- short posterior ciliary vein; *vcp*- vessels of ciliary process; *vi*- vessels of iris; *vns*- vessels of optic nerve and sheath; *vv, vv*- vorticose veins.

b, surface view of portion of choriocapillaris from fundus. × 65. Redrawn from Salzmann. The black spots mark the junctions, with the capillary net, of small connecting arteries and veins.

c, surface view, from inner side, of portion of ciliary body. After Franz.

c- cornea; *cb*- ciliary body; *cor*- corona ciliaris; *cp*- ciliary processes; *f, f*- minor folds; *i*- iris; *orb*- orbiculus ciliaris; *r*- retina; *s*- sclera.

production of aqueous. This was probably not their primary function when they were originally evolved, however, as will be seen later when the method of accommodation in the reptiles is explained. Over the ciliary body, the blind pars ciliaris retinæ consists of a double layer of tall cells, the ciliary epithelium (Fig. 7g, *ce, ce*). The outermost of these layers is pigmented and is a simple continuation of a similar pigmented layer which, further posteriorly, lies between the chorioid and the sensory

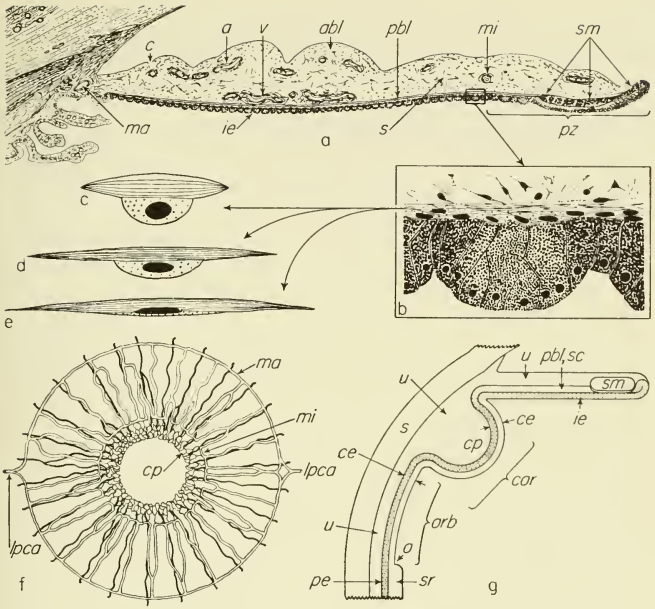

Fig. 7—The iris.

a, radial section of human iris. × 24. *a-* artery; *abl-* anterior border layer; *c-* crypt; *ie-* iris epithelium (= pigmented posterior layer of iridic retina); *ma-* major circle (circular artery in ciliary body); *mi-* minor circle (anastamosis of radial vessels); *pbl-* posterior border layer (= dilatator pupillæ, = myoid lamina of anterior epithelial layer of iridic retina); *pz-* pupillary zone (remainder of iris constitutes ciliary zone); *s-* connective-tissue stroma; *sm-* sphincter muscle; *v-* vein.

b, = the small rectangle in a, enlarged to show the heavily pigmented posterior epithelium and the lightly pigmented 'spindle cells' of the anterior epithelial layer, whose muscular portions merge into a sheet to form the dilatator. Partly after Salzmann.

c, a spindle cell from the anterior retinal layer of the iris of a rhesus monkey, showing the epithelioid cell-body and the partial differentiation of the base of the cell into a muscle fiber, which is shown in its contracted condition. Redrawn, modified, after Hotta. d, same as c, relaxed. e, same as c, but stretched (as when sphincter contracts).

f, diagram of vascular plan of mammalian iris, showing veins in black, arteries clear. *cp-* capillary plexus of pupillary zone (devoted particularly to the sphincter muscle); *lpca, lpca-* long posterior ciliary arteries; *ma-* major circle; *mi-* minor circle.

g, diagram showing distribution of pigment (stippling) in the retinal portion of the iris, as compared with that in the ciliary epithelium and in the region of the sensory retina. *ce, ce-* ciliary epithelium; *cor-* corona ciliaris; *cp-* ciliary process; *ie-* iris epithelium; *o-* ora terminalis of sensory retina; *orb-* orbiculus ciliaris; *pbl, sc-* posterior border layer (= dilatator) and spindle cells; *pe-* pigment epithelium of sensory retina; *s-* sclera; *sm-* sphincter muscle; *sr-* sensory retina; *u, u-* uvea.

part of the retina throughout their extents. The innermost of the two layers of the ciliary epithelium is unpigmented and is a forward continuation of the sensory retina, which drops sharply in thickness at the ora terminalis (Fig. 3; Fig. 7g).

At the anterior end of the ciliary body the uveal tract bends sharply inward, away from the fibrous tunic, to form the iris (Figs. 3, 5, and 7). This structure is an opaque disc of tissue with a hole, the pupil, in its center. It is not flat, but bulged slightly forward by the lens which lies behind it, so that the iris forms a low truncated cone when seen in profile. The periphery of the iris is anchored to the inner aspect of the limbus corneæ by a connective-tissue meshwork, this region being known as the iris- or filtration-angle (Fig. 5, *mt, fa*). It is important that this crevice between iris and cornea remain wide, and not be squeezed shut or blocked by material of any kind. This would lead to glaucoma, for the only important exit-pathway for excess fluid, the canal of Schlemm (Fig. 3; Fig. 5, *sc*), lies shallowly embedded in the fibrous tunic at the iris angle, separated from the aqueous only by a thin layer of the meshwork tissue.

In the iris, the uvea and retina are even more intimately associated than in any part of the ciliary body. On the posterior surface of the iris —that is, the surface directed toward the lens and the vitreous—the relations of the pigmented and unpigmented layers of the double retinal epithelium (here called the pars iridica retinæ) are reversed; for here it is the innermost or posterior layer, nearer the lens, which is pigmented. The anterior or outer layer, toward the cornea, contains little or no pigment (Fig. 7g). In blue eyes, the brown pigment of the retinal backing of the iris is the only pigment the iris contains—the blue color of the iris being caused by optical trickery similar to that which makes veins, containing dark red blood, appear blue when seen through white skin. In brown and black irides, there is more or less pigment also in the uveal connective-tissue stroma of the iris (Fig. 5, *is*; Fig. 7a, *s*), which is much like the chorioid in construction. Inasmuch as the usual color of the mammalian iris is brown, and the human blue eye represents a failure to develop stromal pigment, the blue eye may properly be considered an abnormality—a developmental anomaly—despite its common occurrence. This viewpoint is strengthened by the fact that blue eyes are recessive to the darker colors in heredity. The reader is not advised, however, to refer slightingly to the azure orbs of his inamorata! Perfect albinos (which perhaps never occur in the human species) of course lack even

the retinal pigment, hence have pink irides owing to the easy visibility of the numerous blood vessels of the iris.

The Pupil—The function of the iris is to 'stop down' the lens (Fig. 2) —to prevent the light coming in through the peripheral zone of the cornea from passing through the edge of the lens and reaching the retina. Only the central part of the lens is optically good, and within certain limits the image on the retina will be sharper, the smaller the aperture in the iris. At the same time, the image will be less bright with a smaller pupil, and in a given illumination might not be intense enough to affect the retina unless the pupil could be opened more widely. A wide dilatation of the pupil affects the illumination of the image more than its area or the size of the visual field it subtends; but this increase in image brightness entails a sacrifice of the clarity of the picture, owing to the optical imperfection of the lens periphery which is brought into play.

The regulation of the size of the pupil, in sympathy with the variations in the sensitivity of the retina and the external illumination, is accomplished by contractile elements in the iris. Some of these are full-fledged involuntary muscle cells, indistinguishable from those of the abdominal organs, and are organized into a ring-shaped 'sphincter pupillæ' embedded in the iris stroma and closely surrounding the pupil (*sm* in Figs. 5, 7a, 7g). Contraction of this muscle reduces the diameter of the pupillary circle, though of course there is an obvious minimum below which it cannot be further reduced; so, a circular pupil like that of man cannot be closed entirely. The antagonist of the sphincter is a complex consisting of the elasticity of the tissue and the radial blood vessels (Fig. 7f) of the iris (which are straightened out when the sphincter contracts and which tend to return to an undulant resting shape) together with the active contractility of the 'dilatator pupillæ'. This latter (Fig. 7a, *pbl*; Fig. 7b-e) is not a true muscle, but a myoid lamina developed from the anterior face of the pars iridica retinæ: the sparsely pigmented cells of the anterior layer of this epithelium have each a long spindle-shaped portion containing contractile fibrillæ and lying with its long axis at right angles to that of the cell body, which is attached to the middle of the spindle (Fig. 7b-e). These spindles thus form a layer which apparently lies alongside the anterior layer of epithelium (Fig. 7a, *pbl*) in the pars iridica retinæ, but is really a part of that epithelium (Fig. 7g). The spindles may even be fused with each other in a syncitial fashion, though this point is uncertain. Their myofibrillæ run radially in the iris, so that

their contraction opens up the pupillary aperture, throwing the body of the iris into concentric folds or contraction furrows. The dilatator, being only a part of an epithelial layer, contains no nuclei and no blood vessels, nor any connective tissue forming septa within it or a sheath outside it. The sphincter shows all of these features, however.

Both sphincter and dilatator are derived embryologically from the anterior layer of the double epithelial pars iridica retinæ which is, embryologically, the zone of the optic cup nearest its lip. The cells which become sphincter muscle fibers separate completely from the epithelium late in fetal life, and the epithelium exhibits a gap underneath them (Fig. 7a, g); but the dilatator cells remain permanently, so to say, in a halfway stage of conversion from epithelium into muscle. As a rare anomaly in man, even this development may fail and there may be no trace of a dilatator, the pupil then remaining strongly contracted throughout life ('microcoria'). Wherever among the lower animals the dilatator is lacking (the pupil then being opened by the elasticity of the iris tissue alone, upon relaxation of the sphincter) the spindle cells of the anterior layer of the pars iridica retinæ remain wholly epithelial, like the cells of the posterior layer, and fail to lose their pigmentation during development as do the elements which produce dilatator fibers in other animals and man.

The sphincter and dilatator have very different nerve supplies from the autonomic system, and respond very differently to pharmacological agents and to substances which duplicate or imitate the natural chemical intermediators between nerve and muscle. They are involved in a number of reflexes. The fundamental one is the contraction of the pupil to protect the retina from dazzlement when the external illumination is suddenly increased. As the retina adapts to the new illumination (by reducing its sensitivity) the pupil slowly reopens. Other reflexes include the 'consensual' contraction of the pupil of a covered eye when the other eye is illuminated, its dilatation in emotional states or when the skin of the neck is pinched, its contraction when the eyes converge and accommodate for nearby objects, etc. The last-mentioned of these reactions is not a true reflex, but the result of co-innervation of the sphincter pupillæ and the muscles of accommodation, the common nerve also running with that which supplies the convergence-muscle, the internal rectus. The complexity of some of the pupil reflexes is only realized when an attempt is made to analyze their neurological basis in cases where the reflexes have been lost or altered, due to traumatic or pathological lesions in the central nervous system.

The Lens and Zonule—The crystalline lens is a glassy, cushion-shaped body which lies behind the iris (Figs. 3 and 5). It is supported from behind by the vitreous body and from the front, to some extent, by the iris. The slightly conical form of the iris is entirely owed to the light pressure of the lens against it. If the lens is removed, as in an operation for cataract, the iris thereafter hangs loosely and trembles whenever the eye moves.

The chief support of the lens is given by a great number of firm threads which, like so many guy-ropes, run from the rim of the lens to the ciliary body. Collectively, these threads form the suspensory ligament or zonule of Zinn (Fig. 3; Fig. 5, *zf*). Each zonule fiber arises from the surface of the ciliary epithelium, runs forward between two adjacent ciliary processes, and sweeps around toward the lens equator to fuse with the capsule of the lens. The largest number of fibers insert on the anterior face of the lens near the equator, a rather smaller number on the posterior face, also near the equator; and scattered fibers insert at the equator everywhere between these anterior and posterior sheets of fibers ('anterior and posterior leaves of the zonule'). Some atypical fibers cross each other between the zonule leaves, and others run from one ciliary process to the next and do not join to the lens at all. A little behind the posterior zonule leaf (which is bowed to fit its curvature) lies the anterior membranous surface of the vitreous, which is joined to the posterior lens capsule along a narrow ring (Egger's line; Fig. 5, *el*) but is free of the posterior lens surface in its center, creating the fluid-filled 'retrolental space' (Fig. 3; Fig. 5, *rs*). Between the anterior hyaloid membrane of the vitreous and the posterior leaf of the zonule is the flattened annular 'canal of Petit'. Between the leaves of the zonule is the space called the 'canal of Hannover'—though of course it is not a true canal since the fibers in each leaf of the zonule do not form an intact membrane, but rather a grille. Between the anterior leaf and the back of the iris lies the posterior chamber *sensu stricto* (Fig. 5, *pcs*), although the term 'posterior chamber' is properly enough used to embrace collectively all of the aqueous-filled spaces behind the iris.

Newly-formed aqueous, poured into the posterior chamber by the ciliary epithelium, can get into the anterior chamber (between iris and cornea) only by infiltrating between the zonule fibers and then passing between lens and iris and through the pupil. If, in an inflammation of the iris, the whole pupil margin adheres to the lens capsule, the aqueous

accumulates in the posterior chamber and bulges the iris forward, this being one of the many possible causes of glaucoma.

The body of the lens, released from its capsule in the fresh condition, is a glutinous, almost inelastic mass which gives no hint of its true histological structure. This is best disclosed by crushing a lens which has been hardened in formalin or alcohol, when it is seen that the lens is composed of innumerable layers, like the coats of an onion, each layer in turn being made up of fine fibers. An individual lens fiber in a given layer runs from an anterior point, near the axis of the lens, circumferentially around to a point in the posterior half of the lens—again near the axis. No fibers could each have both ends exactly on the lens axis, or the lens would be greatly elongated, pointed anteriorly and posteriorly, and would then be quite unsuited to its optical function. Fibers running in one radius or meridian of the lens meet fibers in the diametrically opposite meridian, end-to-end, along radial planes called 'lens sutures' (see Chapter 5, section A; Figs. 40, 41, pp. 110-1). These suture planes necessarily branch more and more elaborately as the lens body grows by the addition of new layers of fibers at its surface, in order to accommodate the increase in number of fibers in each layer over the smaller number in the next innermost, slightly older layer. A given lens fiber tends to lie along the convex curvature of a fiber in the next innermost layer of fibers, and along the concave curvature of one in the next outermost layer. Radial lamellæ of fibers are thus built up so that the lens, besides having an 'onion' aspect, can also be thought of as being built like an orange with many hundreds of segments. Since the diameter of a single fiber is quite constant, the number of fibers per layer increases as the lens grows, and the number of radial lamellæ perforce increases from time to time so that a maximum can be counted at the surface, fewer and fewer farther and farther in toward the center of the lens.

The lens is contained in an unbroken, homogeneous, elastic envelope, the lens capsule. The capsule is not uniform in thickness everywhere but has definite thickened zones at particular locations, whose importance will be explained in connection with accommodation. Covering the anterior half of the lens, to and slightly beyond the equator, is a single layer of cuboidal cells, the lens epithelium (Fig. 5, *le*). This layer lies just beneath the capsule. It is of no importance optically, but is all-important for the growth of the lens. It is believed to secrete the capsule or at least to be more efficient in this than the lens fibers which have their sides against the posterior half of the capsule, for the anterior por-

tion of the capsule is thicker than the posterior in most animals. This is, however, open to interpretation as a positive adaptation rather than a mere accident of difference in secretory capacity, for as will be seen later, accommodation is facilitated by a thick anterior capsule but would be indifferent toward an equally thick posterior capsule.

The lens epithelium is the source of all of the myriads of lens fibers excepting a very small ball of them at the center of the lens, which are formed directly from the posterior wall of the embryonic lens vesicle—a bubble of tissue which forms as a pit in the skin of the head, from which it closes off and pinches free to sink down into the optic cup. If the lens epithelium could be isolated intact, it would be like a thin, shallow bowl composed of tiny tiles. We must imagine this bowl to be growing constantly by the multiplication of its tiles, with those at the edge of the bowl elongating into rods which, as they get longer and longer, each slide one end along the inner surface of the bowl toward its center, the other end growing in the opposite direction and curving toward a point in space above the center of the bowl. It is in this fashion that each new layer of lens fibers is added over the preceding one (Figs. 40 and 41), by the conversion of the epithelial cells at the equator of the lens into long, curved threads which are hexagonal in cross-section so as to fit against one another without intervening space, just as do the cells of the epithelium itself. Any given cell in the epithelium of a growing lens is thus moved steadily toward the lens equator by the mitotic expansion of the epithelium, and, upon finding itself eventually at the rim of the epithelial bowl, proceeds to convert itself into a lens fiber.

The lens is very prone to opacify, thus giving rise to 'cataract', in response to any of a number of causes; but it is normally optically empty—that is, completely transparent and with no obvious signs of its elaborate internal structure. With special lighting arrangements, as with the ophthalmologist's slit-lamp, it is possible to see several concentric surfaces within the lens, analogous to growth-rings in a tree trunk. These mark periods in life—the same in all of us—at which the optical density of the new-forming lens fibers is changed abruptly to a lower value than that of the previously formed layers of fibers. Thus the optical density of the lens—its effectiveness in slowing the speed of light and hence its focusing power—decreases in several distinct steps from center to surface. In a given region, however, the density of the fibers and of the scant fluid between them is so nearly identical that the surfaces of the

fibers reflect no light and consequently are invisible in the living lens. The fibrous structure of the lens simply disappears as does a glass bead when dropped into a vial of oil of the same optical density as the glass.

(B) Optics and Accommodation

Refraction—The property of substances which is called their 'optical density' has been alluded to above. The higher the optical density of a material, the slower light is able to travel through it. Light travels fastest through a vacuum and very nearly as fast through air, so that for practical purposes the speed of light in air is taken as the maximum. This speed divided by the speed of light in a given substance gives a figure

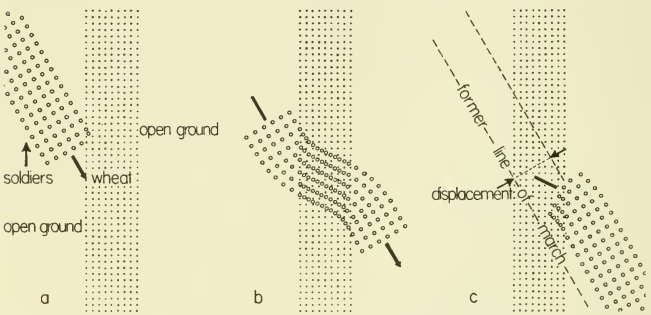

Fig. 8—An analogy for the refractive bending of light rays by a glass plate (see text).

which is called the 'index of refraction' of that substance referred to air as a standard.

The effect of the optical density of a substance is to produce a bending of a beam of light which enters that substance at an angle, having previously traversed a substance of different optical density. The amount of the bend in the light-beam will depend upon the difference in optical density of the two substances and upon the angle at which the beam approaches their interface. The direction of bending will depend upon whether the second substance traversed has a higher or lower density, or index of refraction, than the first.

This bending of light rays when they pass through boundary surfaces is called 'refraction'. Its basis may be best understood if we use an old

favorite analogy for our light-beam and our pair of optically different substances. Suppose a platoon of soldiers to be marching over bare ground toward the edge of a wheat-field, which is at an angle to their line of march (Fig. 8). The ranks of soldiers now represent successive wave-fronts in a light-beam, and their files represent the individual light rays in the beam. Obviously the soldiers cannot march as fast through the dense wheat as over open ground, so that the latter may represent air, and the wheat-field a piece of glass of high optical density.

As the first soldiers in the front rank start into the wheat, they are slowed up, but those at the other end of the front rank are still able to

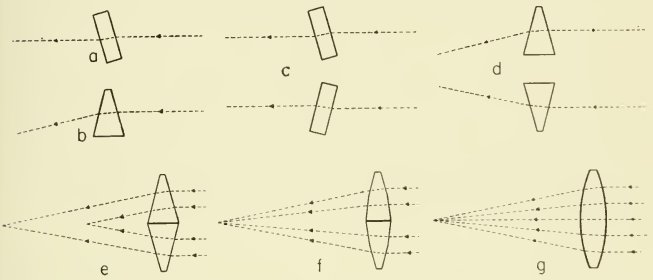

Fig. 9—Step-by-step explanation of the focusing of parallel rays by a convex lens.

a, displacement of ray by tilted plane-parallel plate (compare Fig. 8). b, bending of ray by prismatic plate. c, approximation of parallel rays without convergence, by pair of tilted plane-parallel plates. d, convergence of parallel rays by pair of prismatic plates. e, independent foci of pairs of parallel rays, through action of prisms placed base-to-base. f, coincidence of foci when slope of prism faces is decreased toward their bases. g, single focus of all parallel rays, resulting when process in f is fully carried out, yielding a smoothly-curved lens.

march rapidly since they have not yet reached the wheat (Fig. 8a). Consequently the front rank is swung around as if hinged at one end, and by the time the whole of the rank is in the wheat, it has taken a new direction of march which is of course followed by each rank in the whole platoon (Fig. 8b). Upon emerging from the wheat-field on the other side (Fig. 8c), the process is reversed and the platoon's line of march becomes parallel to its original one, displaced laterally a distance which depends upon the width of the wheat-field and the difficulty of marching through it.

If the soldiers had encountered the wheat head on instead of at an angle, their line of march would not have been tilted. But their ranks would have been closed up, and while moving through the wheat each soldier would have been treading on the heels of the man in front of him. Strictly speaking, this would be refraction also, for the same decrease in wavelength occurs when the angle of incidence is other than 90°—refraction is most accurately defined in terms not of any bending of the light rays, but of their change in speed and wavelength. Thus it actually takes place when light meets a surface at right angles; but since no *visible* change then occurs, the existence of the phenomenon is more or less ignored.

Substituting now our beam of light and piece of glass for the soldiers and the wheat-field, we can understand why the angle at which the light meets the glass is so important in determining the direction the beam will take through the glass. If the angle be changed, the new direction will change. If a perpendicular be drawn to the surface of the glass, then the beam of light on entering the glass from air will be bent toward the perpendicular; and upon escaping from the glass into air again it will be bent away from a perpendicular at the point of escape, the two bends in the beam being equal if the two surfaces of the glass are parallel.

Action of a Convex Lens—We are now ready to understand how a lens brings rays of light to a focus (study Fig. 9). If a beam of parallel rays of light strikes a convex lens, each ray in the beam will make an angle with a tangent to the lens at the point where the ray strikes it, and the angle will vary with the distance of the ray from the central ray of the beam, which we will suppose to pass through the center of curvature of the lens surface. The farther a ray is from the axial (central) ray, the greater the angle it makes with a radius of the lens at its point of contact with the latter, and the greater the angle of bending, *toward* the radius, through which it will be refracted by the glass of the lens (Fig. 9g).

Thus, the outermost rays of the beam are bent the most, rays lying closer and closer to the axial ray are bent less and less, and the axial ray is not bent at all. All the rays thus converge beyond the lens and if the shape of the lens surface is just right, they may be made to converge at a single point. This point, or 'focus', will be at a fixed distance from the lens, and that distance can be varied only in two possible ways —by making the lens variable in curvature or by exchanging it for a

different one. About the only *variable* lenses in the world are those in living vertebrate eyes.

A lens forms an 'image' of an object, the distance of the image from the lens being fixed as long as the distance of the object from the lens is constant. We can best grasp how the image is formed if we think of it as being made up of a large number of points, each corresponding to a point on the object (Fig. 10). The light reflected from each point on the object—its two end-points, say, as in Figure 10—travels in straight lines away from that point in all possible directions unless the object happens to have a mirror-like surface. We can be sure of this, for we can walk around an object and see it, from any direction, by means of

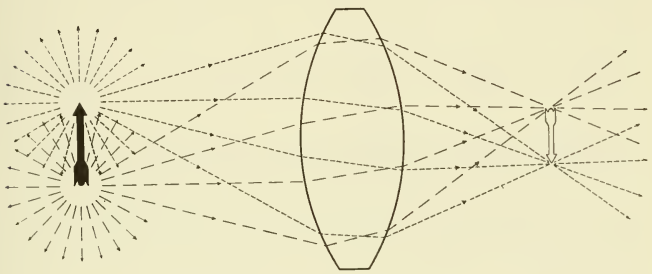

Fig. 10—Formation of an image by a lens.

Of the rays emanating in all directions from each point on the object, those intercepted by the lens are brought to a focus, thus generating a point in the image. Each image-point lies on the opposite side of the lens axis from the corresponding object point; hence the image is inverted.

the light coming in that direction from the object to our eyes. All of the rays from an object-point which happen to be intercepted by a lens are brought to a point focus beyond the lens at a particular, fixed distance. If the object-point lies below the axis of the lens, however, the light from it will be focused at an image-point above the axis and vice versa. Hence, when we consider all the image-points formed by the focusing of all the light from each of the object-points, we understand how the image is built up. We also see why it hangs in space at a fixed distance from the lens, is smaller than the object, and is inverted. We can now *see* the image if we catch it on a screen at the image-distance from the

lens. If we move the screen toward or away from the lens the image will immediately become blurred because the object-points will be represented on the screen not by sharp image-points, but by patches of light of the same shape as the lens ('blur' or 'confusion' circles, where the lens is round) which overlap each other.

If the screen now remains stationary at the proper distance, and the *object* moves toward or away from the lens, the image will focus behind or in front of the screen (Fig. 11), and the picture on the latter will again be composed of hazy blur circles. With the object in this new position, its image can now be made to fall on the screen only if the lens is shifted in position or altered in curvature. Both of these methods are used, in different kinds of vertebrate eyes, to keep the image sharp on

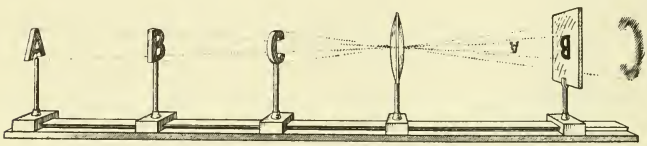

Fig. 11—Relation of object-distance to image-distance. After Kahn.

Only the B is sharply imaged on the screen, on which the A and C are represented by blurs. The sharp images of the A and C hang in space as shown, and can be placed on the stationary screen only by moving the lens, or by substituting another lens of different strength.

the retinal screen when the object varies in distance from the eye. These adjustments comprise what is called 'accommodation'.

Refractive Errors of the Eye—In the human eye there are several curved surfaces at which refraction takes place, the end result being the production of an image on the retina. There is also an elaborate arrangement for changing the curvature of one of these surfaces so that the image can be moved slightly forward or backward in the eye. This mechanism of accommodation comes into play when we shift our gaze from a distant to a nearby object, or when we watch an object which is moving toward or away from us. As an object approaches, its image recedes behind the retina and must be pulled forward. As an object goes away from us, its image moves forward into the vitreous and must be pressed back onto the retina in order to be seen sharply. In many persons the eyeball is abnormally short (Fig. 12, top diagrams), so that the

accommodation process, unaided by convex spectacles, is inadequate to pull the image forward onto the retina and the sharp picture lies behind the eye (hypermetropia or far-sightedness). In others, the eyeball is abnormally elongated (Fig. 12, bottom diagrams) and the image lies so far forward in the vitreous (except when the object is very close to the eye) that concave spectacles are required to move the focus of the lens backward and place the image on the retina (myopia or near-sightedness).

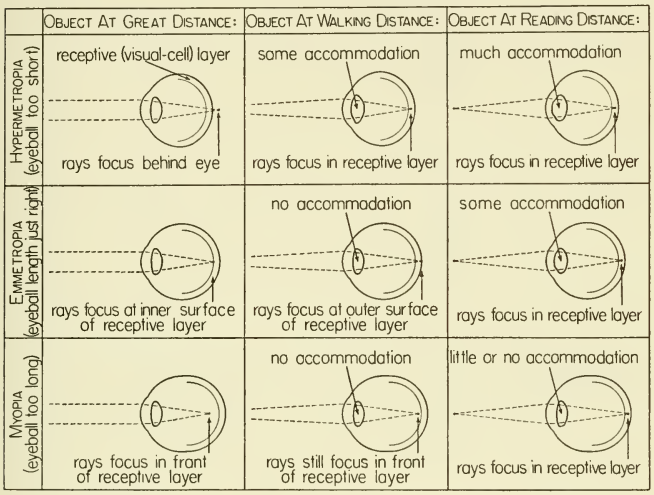

Fig. 12—Spherical refractive errors of the eye.

Shows the extent of accommodation required, and the location of the images, in hypermetropic or far-sighted eyes (top row), normal eyes (middle row), and myopic or near-sighted eyes (bottom row).

A third refractive error to which the human eye is prone is 'astigmatism', a condition in which the retinal image of a point is not a point but a line, owing to one of the refracting surfaces (almost always the cornea) being partly cylindrical as well as spherical in its curvature (Fig. 13). This results in a blurring of objective lines running in certain directions. The error is easily corrected, when it is regular as indeed it usually is, by the appropriate counteracting cylindrical curvature formed on the

spectacle lens. As we shall see later, all three of these conditions which for the human eye are 'errors', are perfectly normal and desirable situations in the eyes of various vertebrates whose visual requirements differ greatly from our own.

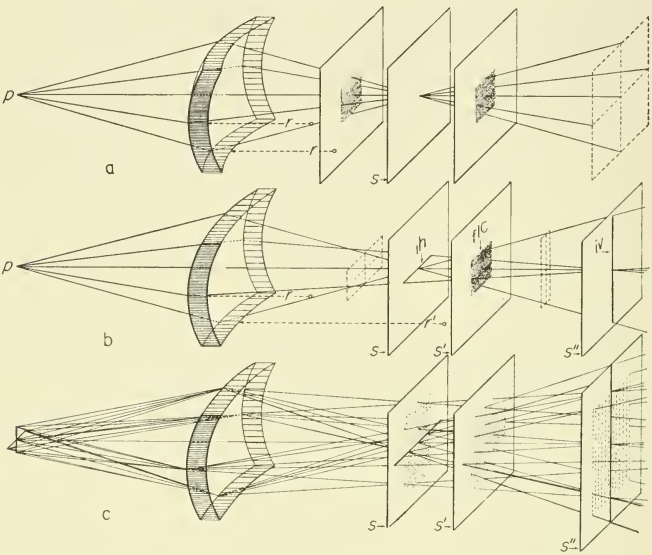

Fig. 13—Astigmatism.

a, a square piece of normal cornea whose radius of curvature, *r*, is the same in all meridians, images a point *p* as a point on the screen *s*. In any other position the screen would intercept a blur-square.

b, a piece of cornea whose radius of curvature in one direction, *r'*, exceeds its radius of curvature in another direction, *r*, is said to be astigmatic. It images a point *p* as a line (horizontal in this instance) *ih* on a screen *s* placed in its first focal plane, and also as a line at right angles to the first (the linear vertical image *iv*) on a screen *s''* placed in its second focal plane. The most compact image of *p* is the 'figure of least confusion', *flc*, on the screen *s'*; but this image is a blur-square—the point *p* is nowhere imaged as a point, as in a.

c, the same piece of astigmatic cornea as in b sharply images the horizontal limbs of a cross on the screen *s*, places a blurred cross on the screen *s'*, and sharply images the vertical limbs of the cross on the screen *s''*. The whole of the object cannot be sharply imaged at any one distance from the astigmatic refracting structure.

Dioptrics of the Normal Eye—As light enters the eyeball it first encounters the tissue of the cornea, then in succession the aqueous humor, the lens, the vitreous humor and the transparent retina on whose posterior, outer surface the sensory rod and cone cells lie. These transparent structures and substances, exclusive of the retina, are known collectively as the dioptric media. When a light ray comes through the air into the cornea at one side of the latter's center, it is bent sharply toward the antero-posterior axis of the eyeball. Upon leaving the cornea and entering the aqueous humor, the ray is bent again but only very slightly since the corneal tissue and the aqueous have nearly the same optical density. The refractive index of the cornea is 1.376, and that of the aqueous is 1.336, which is about the same as that of water.

Now upon entering the lens, the ray is bent further, again toward the axis of the eye. The index of refraction of the lens can be taken as 1.42. Actually, the values for the lens are 1.406 at the center, 1.386 at the surface, but because of its zoned structure the lens behaves as would a homogenous body whose index was actually higher than that of any part of the lens. This figure, 1.42, for the effective index of the lens, does not exceed the index of the aqueous (1.336) by as much as the latter value exceeds the index of air (1.00). This, together with the fact that the anterior surface of the lens is not as sharply curved as the cornea, is responsible for the fact—often overlooked—that the *cornea* does most of the job of placing the image on the retina. In the optically normal eye the lens acts like the fine adjustment of a microscope—it adjusts the position of the image only in a minor way. Some highly myopic persons, in fact, see clearly without spectacles after the lens has been removed because of cataract—with the lens in the eye, they have too much focusing power, the focal length of the cornea alone being equal to the length of their abnormally elongated eyeballs.

Upon travelling through the posterior surface of the lens into the vitreous humor, our light ray for the first time passes from a medium of higher density into one of lower density—the vitreous having the same index as the aqueous. If it were passing through a convex surface, it would be bent away from the axis of the eye; but since it is here travelling through a *concave* surface it is still further converged toward the axis. In fact, since both surfaces of the lens are in contact with media whose refractive indices are the same, and the posterior surface of the lens is more sharply curved than the anterior, the posterior face is the more important of the two in the static refraction of the eye.

The ray now travels to the retina, having crossed the optic axis of the eye so that it strikes the retina on the opposite side of the axis to the one on which it entered the cornea. The retinal image of an object is consequently inverted and much smaller than the object, as is true of the image of any simple convex lens, as we have seen. The refractive index of the human retinal tissue, which in life is optically empty, is not known; but it may be of considerable importance in connection with the physiology of the fovea (Chapter 8, Section C). There are indications that it is higher than that of the vitreous and may approach that of the lens.

It should be borne in mind that it is the difference in refractive index on the two sides of a boundary surface which, together with the sharpness of curvature of that surface and the direction of curvature (whether convex or concave), determines the extent of convergence or divergence of light rays passing through it. The absolute values of the refractive indices are of no consequence. Hence since the anterior surface of the cornea is an interface between two very different media (air and tissue) it is the most important refractive surface in the dioptric media. The posterior surface of the lens is next in importance, the anterior surface of the lens least effective (when the eye is not accommodating), and the posterior surface of the cornea can be ignored entirely.

It is the anterior surface of the lens, however, which in the human eye is alone modified in curvature in the act of accommodation—hence for this process, that surface is of paramount importance. We are now prepared to examine the mechanism by which human accommodation is accomplished.

Accommodation—In the first place the reason for accommodation, and the extent of the process, need to be clearly understood. The curvatures of the refractive surfaces of the ideal human eye and the refractive indices of ordinary air and of the dioptric media are such that when the eye is at rest—that is, exercising no muscular effort to accommodate for nearby objects—objects at the horizon are in focus upon the back surface of the transparent retina. The seeing-cells, the rods and cones, stand on this surface like the bristles of a brush. Their length is appreciable, and since a light ray which helps to form the image strikes the retina perpendicular to its surface and thus passes axially through a visual cell, it follows that the optical image may lie anywhere along the length of the visual elements and still form the same photochemical image, and be as sharply 'seen' in the form of a cerebral or mental image.

There is thus a certain leeway which the focus of the optical image may have without its becoming blurred in the consciousness. This leeway is in fact so great that without any change in the dioptric structures of the eye, an object can approach from the horizon to a distance of about twenty feet* without its image moving back far enough to get out of the visual-cell layer and into the insensitive chorioid. The image in the eye is so very small compared with the object that since the *movement* of the image, either laterally or forward and backward, is minified to a high degree, the movements of the image over the surface of the retina (especially through its thickness) are almost microscopic. Conse-

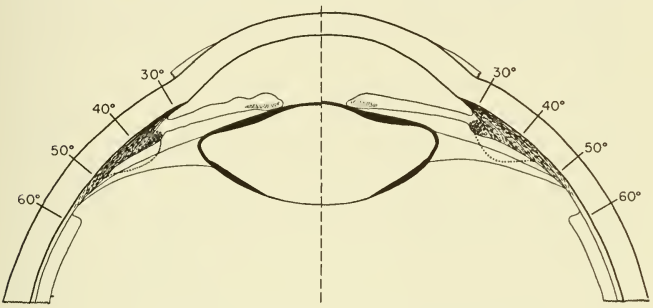

Fig. 14—The mechanism of human accommodation.

The left half of the diagram shows the structures in relaxation. The thickness of the lens capsule has been exaggerated one hundred times to bring out its local variations. On the right, accommodation; by reference to the angular scales, the movements of the various parts can be discerned. Note that the contraction of both the radial and circumferential portions of the ciliary muscle has stretched forward the smooth orbicular region of the ciliary body (to which most of the zonule fibers attach) and has bunched up the coronal region (bearing the ciliary processes, whose profiles are indicated by the dotted lines). The relaxation of the zonule fibers has permitted the elastic lens capsule to mold a bulge of sharpened curvature on the anterior surface of the lens. Note also that the sphincter muscle of the iris has contracted, closing down the pupil in its 'accommodation reflex'.

quently, the object may recede from twenty feet to infinity without its image coming forward more than the length of the rods and cones—a small fraction of a millimeter (see Fig. 19, p. 43).

Within twenty feet, however, the refracting power of the media must somehow be increased to keep the image in the visual-cell layer of the retina. In the human, the anterior surface of the lens is sharpened in

*It is really a bit more, but so variable that for the didactic purposes of this book, twenty feet is arbitrarily taken as standard.

curvature to accomplish this (Fig. 14), and the structures most involved are the lens capsule, the zonule fibers, and the muscle cells in the ciliary body. The latter must contract to focus the eye for nearby objects, relax partially for more distant objects up to twenty feet away, and relax completely for objects beyond twenty feet. This is why it is restful to the eyes to gaze out of a window at distant objects for a few moments occasionally, when doing close work of any kind.

The ciliary muscle fibers are formed into two muscles which blend with each other and are really only one, since one mass of fibers is derived from the other in the embryo and the two masses have a common nerve supply and act together, having the same effect upon accommodation in spite of their great difference in orientation within the ciliary body.

The 'radial' or 'meridional' fibers, as seen in a sagittal section of the eye, are arranged fanwise, the small end of the mass being fastened at the scleral roll and the other end being frayed out and distributed along the whole ciliary body, most of the fibers ending along its inner surface (Fig. 3; Fig. 5, *mb*). When this radial muscle (of Brücke) contracts, the effect is a stretching of the flat orbiculus region of the ciliary body so that its anterior border moves forward—the ora terminalis being fixed. The corona ciliaris, that portion of the ciliary body bearing the ciliary processes, is telescoped, its posterior border moving forward but its anterior attachment at the iris angle remaining fixed. The result of this forward movement of the region of junction between corona and orbiculus is a relaxation of the taut guy-wires of the lens, the zonule fibers. These are normally in a state of considerable tension when the ciliary muscle is *not* contracted; for, as the eyeball grows, before and after birth, its diameter increases proportionately faster than that of the lens. Hence the suspensory-ligament fibers, once they have grown out from the ciliary epithelium and attained connection with the young lens capsule, are placed under constantly increasing lengthwise stress which is not entirely removed by any compensatory increase in length on their part. This brings about a slow broadening and flattening of the growing lens and a permanent state of tension in the suspensory ligament, which can be relieved only by the contraction of the ciliary muscle.

A portion of the ciliary muscle fibers, the number being often greater in far-sighted eyes and less in near-sighted ones (where they may even be entirely lacking) are organized into a ring-like muscle (of Müller), analogous to the sphincter pupillæ. Although the fibers in Müller's muscle

(Fig. 5, *mm*) are thus at right angles to those of the radial (Brücke's) muscle, the two muscle masses are in no way antagonistic in their action as are the sphincter and dilatator pupillæ. The contraction of Müller's muscle heaves the ciliary processes inward toward the axis of the eyeball and thus substantially supplements the action of Brücke's muscle in letting up the tension in the zonule fibers. In fact, the muscle of Müller is much the more efficient of the two, since no component of its direction of contraction is wasted in uselessly pulling any part of the ciliary body *forward* in the eye. It is only the *inward* component of the action of the diagonally-placed Brücke's muscle which is very useful. It is significant that in far-sighted (hypermetropic) eyes, which must constantly make extra accommodatory effort (Fig. 12), it is Müller's muscle—not Brücke's—which becomes hypertrophied if spectacles are not worn.

To understand what happens to the lens when the zonule is relaxed, we must recall the nature of the lens capsule and consider its structure in a little more detail. The capsule is a firm, elastic membrane. If a cut is made in it, the edges of the cut will tend to roll outward—thus it is clear that the capsule is normally exerting pressure on the lens fibers. If the capsule were equally thick throughout and the lens fibers were plastic enough, the elasticity of the capsule would tend to mold the lens into a ball if the flattening effect of the tensed zonule fibers were to be eliminated by cutting them.

Actually, however, the capsule varies greatly in thickness in different parts and consequently varies locally in the force which its elasticity can exert upon the lens capsule (Fig. 14). Fincham, who has revised and modernized the Helmholtz theory of human accommodation, has carefully studied the properties of the capsule and of the decapsulated lens. Without its capsule, the body of the lens slowly takes on the flattened form characteristic of the intact lens *in situ* in the resting eye. Hence the bulged form of the lens in accommodation is brought about by the capsule's assertion, upon it, of a molding force more than strong enough to overcome the tendency of the lens body to flatten. Cutting the zonule fibers allows the capsule to mold the lens into the same shape it has in accommodation. The relaxation of the ciliary muscle allows the tensed zonule fibers to effect a 'physiological decapsulation' of the lens, by pulling so hard upon the equator of the capsule that the latter's elasticity is rendered ineffectual, and the lens body assumes the same flattened form which it takes when removed from its capsule. The contraction of the ciliary muscle, on the other hand, eliminates the pull of the zonule fibers

just as if the latter had been severed and the lens entirely isolated. We may express these antagonisms and coöperations as a series of equations:

Lens − capsule = lens in situ + relaxed ciliary muscles (no accom.);

Lens + capsule − zonule = lens in situ + contracted ciliary muscles;

Lens + capsule − accommodation = lens − capsule;

Lens + capsule + zonule + accommodation = lens + capsule − zonule; and so on.

The thinnest portion of the lens capsule is a large central area of its posterior part. This is surrounded by a greatly thickened band which lies fairly close to the equator. The equatorial region itself is again thin. On the anterior surface is another thickened zone which lies a little farther from the equator than the posterior thickening and leaves a smaller thin central area than occurs on the posterior capsule. This central thin area of the anterior capsule is also slightly thicker than the posterior central thin area (Fig. 14).

Ordinarily all of the light used for vision passes only through the anterior and posterior central thinnings of the capsule—the pupil does not dilate widely enough to expose the periphery of the lens to incoming light. The posterior surface of the lens fits the vitreous body so closely, with incompressible fluid in the retrolental space between the two, that it cannot change its curvature materially during accommodation. The anterior leaf of the zonule is probably relaxed more completely than the weaker posterior leaf at a given stage of accommodation, and the net result is that only the anterior lens surface is free to deform when the zonule is relaxed by the contraction of the ciliary muscles. The anterior zone of thickening in the capsule then proceeds to reduce its diameter and is stiff enough to force the thin central area of the capsule to form a bulge, into which the body of the lens is molded. This sharpening of the curvature of the useful portion of the anterior lens surface increases the refracting power of the eye and holds the image forward on the retina in spite of the approach of the object within the 'commencement point' of accommodation—that is, within the critical twenty-foot distance.

The amount of accommodation which is being exerted at any one time, and the total amount of which the individual is capable, can be conveniently expressed in the same units used for designating the focusing power of a lens. The unit in question—the diopter—is not really a unit at all, for it has a sliding value. The strength of a lens in diopters is the reciprocal of its focal length in meters. That is, a one-diopter lens focuses parallel rays at a point one meter away, and a two-diopter lens

focuses at one-half meter, a five diopter lens at one-fifth of a meter, and so on. The emmetropic eye (Fig. 12, middle row of diagrams) focuses parallel rays on its receptive layer when it is not accommodating. If now a one-diopter lens is added, like a spectacle, in front of the relaxed eye, an object one meter away will be imaged on the retina. A four-diopter spectacle will enable the non-accommodating eye to image sharply an object only a quarter of a meter distant. So, we may say that the amount of accommodation being exerted by an emmetropic eye is four diopters when, without a spectacle, it images an object at one-fourth of a meter.

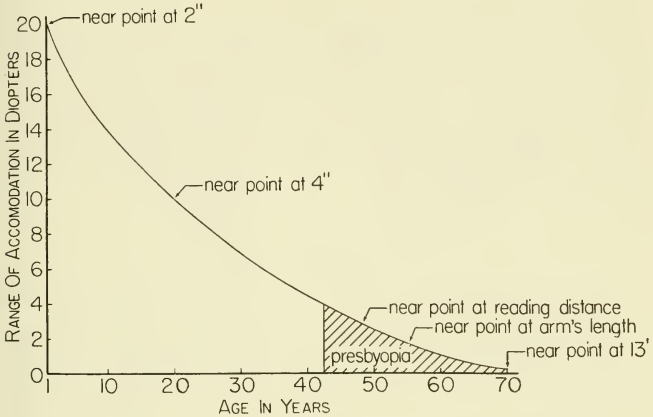

Fig. 15—Decrease of human accommodation with age, owing to the progressive hardening of the body of the lens. Plotted from data of Donders on emmetropic subjects.

By accommodating to a certain extent—four diopters' worth—the focusing power of the crystalline lens has been increased by four diopters over its strength when at rest; for, this amount of accommodation can take the place of a four-diopter spectacle placed before the non-accommodating eye.

The range of accommodation—that is, the greatest increase in the focusing power of the lens—which a person can produce is unfortunately not a fixed quantity (Fig. 15). Almost as inevitable as death and taxes is a decrease in that range, with age, to such an extent that the individual (unless substantially myopic to begin with) becomes unable to

image objects as close as one holds a book to read, and must adopt spectacles whether he has ever needed them before or not. This phenomenon is called presbyopia (literally, old sight), and most of us enter its realm sometime in our forties. The decrease in accommodating power is not caused by any weakening of the ciliary muscle, but by a perfectly normal, progressive hardening of the lens. The ciliary muscle tries as hard as ever in the presbyopic years—but *its* force, be it remembered, is not the one which molds the lens. The actual molding force, the elasticity of the lens capsule, is really quite weak at best, and becomes wholly inadequate to its task when the body of the lens reaches a certain stage of firmness. The hardening of the lens is so gradual, however, that few of us live so long that our graph of the process (Fig. 15) reaches the line of zero accommodation. When this does happen, the once emmetropic eye is still emmetropic—still focuses parallel rays upon its retina; but its 'near point' (the nearest point at which an object can be sharply imaged) has moved away from the eye until it is twenty feet away, at the point where the eye formerly commenced to accommodate for approaching objects.

(C) The Ocular Adnexa

The major anatomical structures which fall under the above heading are the oculomotor muscles, the lids, and the lacrimal apparatus.

The eyeball lies, cushioned by fat, in a pyramidal cavity in the skull, the bony orbit. The angle at the apex of the orbit is about 45°, and the center-lines of the two orbits also make an angle of about 45°. This brings the mesial walls of the orbits approximately parallel; but for the axes of the eyeballs to be parallel it is necessary for them to make 22½° angles with the axes of the orbits.

The Oculomotor Muscles—Back at the apex of the orbit is the small aperture by which the optic nerve enters the skull, and close to this point are the origins of four of the six muscles which rotate the eyeball (Fig. 16). These are the straight muscles or 'recti'—superior, inferior, medial (internal, nasal) and lateral (external, temporal). They form the 'muscle cone' around the nerve and diverge toward the equator of the eyeball. Here they pass through the connective-tissue capsule (of Tenon) which forms a jacket over the sclera, loosely connected to the episcleral tissue, and which is a portion of an elaborate system of connective-tissue membranes or fascia in the orbit, one of whose fortunate

functions is to bar conjunctival infections from the orbit where they might do great damage to the eye and the brain.

Becoming tendinous on passing through Tenon's capsule, the insertions of the muscles fuse with the tissue of the sclera. Since the fascial sheaths of the muscles are continuous with Tenon's capsule, it is possible to dissect a diseased eye out of the capsule, and by sewing a ball into the latter, provide a stump for an artificial eye which will move in harmony with the good eye of the other side.

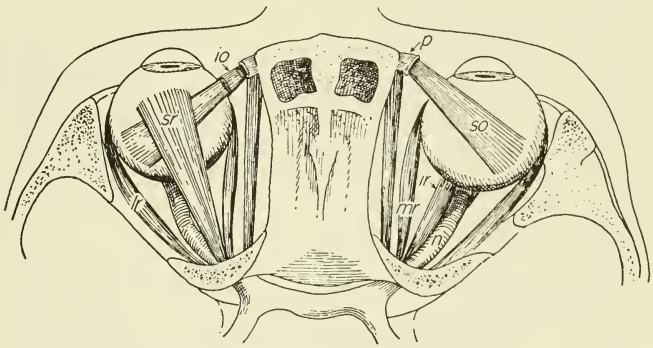

Fig. 16—Oculomotor muscles of man, as seen from above in a dissected head.

On the left, a portion of the superior oblique has been cut away to reveal the inferior oblique; on the right, the superior rectus has been removed to permit a view of the inferior rectus. Modified from Adler.

io- inferior oblique; *ir*- inferior rectus; *lr*- lateral (external) rectus; *mr*- medial (internal) rectus; *n*- optic nerve; *p*- pulley through which tendon of superior oblique passes; *so*- tendinous portion of superior oblique; *sr*- superior rectus.

Two other muscles (Figs. 16 and 17) meet the superior and inferior surfaces of the eyeball obliquely from the nasal side of the anterior part of the orbit, where one of them, the 'inferior oblique' muscle, is attached. The other, 'superior oblique', has however greatly lengthened phylogenetically and its origin has moved back toward that of the recti. Its sidewise attack upon the eyeball was preserved throughout the backward migration of its origin by the development of a tough ring or pulley, through which it passes. The pulley formed at the old sub-mammalian site of attachment of the muscle on the anterior nasal orbital wall. As an anomaly, the muscle may atavistically end here, or a normal superior

oblique may be accompanied between the eyeball and the pulley by an extra muscular slip which has a common insertion with it upon the eyeball. An additional and interesting atavism in an occasional human is a 'retractor bulbi' muscle, which in other mammals serves to hold the eyeball tightly back in the orbit regardless of the relaxations and contractions of the eye-rotating muscles. It ordinarily has four parts in mammals, alternating with the recti and originating with them at the apex of the orbit. The anomalous human retractor bulbi may exhibit this complete arrangement. The two oblique muscles, approaching the eyeball from the nasal side, might seem to give the muscular apparatus extra power for converging the two eyes—convergent movements being more frequent than any others—but since they do not pass in front of the center of rotation of the eye, their chief actions are to tilt the eyeball upward and downward. Their original purpose was, however, very different (p. 303).

The six normal muscles are supplied by three different cranial nerves, one of which cares for four of them. Their bilaterally coöperative actions and the elaborate central-nervous control thereof are beyond the scope of this elementary description.

The Lids—The eyelids are essentially folds of skin, which were developed by land animals primarily for cleaning and moistening the cornea, and which incidentally protect the eye from small foreign objects such as insects, wind-blown sand, and the like. The cornea of an aquatic animal is kept clean and succulent by the water itself, through which no natural particle can travel with sufficient velocity to injure or embed in the cornea. It is a mistake to suppose that the chief purpose of the lids is to protect the eye—from blows, and so on; for they are no real protection against such insults. That function, in man, is taken care of by the supraorbital ridges of the skull which overhang the orbits and bear the eyebrows, whose purpose appears to be to divert sweat from the eyes.

The opening between the lids, which reveals a portion of the eyeball, is the 'palpebral fissure'. Its temporal and nasal angles are respectively the (sharper) outer and (broader) inner 'canthi'. In the inner canthus can be seen the plica semilunaris, a crescentic fold of conjunctiva which is a vestige of a third, sidewise-sweeping eyelid present in many animals, the nictitating membrane. Neither the special muscles nor the special gland (Harder's) of the third eyelid are present, even as vestiges, in man. Overlying the base of the plica is a pink mass, the caruncle, which is really a bit of the margin of the lower lid which becomes isolated

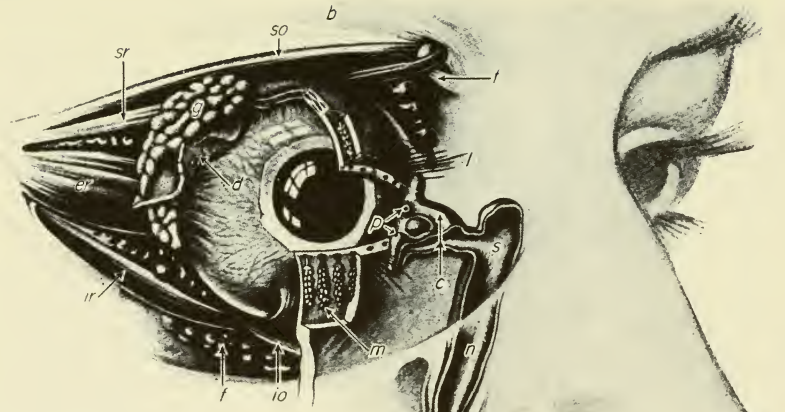

Fig. 17—The adnexa of the human eye. After Kahn. *b*- brow, on bony supraorbital ridge; *c*- canaliculi, embracing caruncle, and leading to lacrimal sac; *d*- duct openings of lacrimal gland; *er*- external rectus; *f*- orbital fat; *g*- lacrimal gland; *io*- inferior oblique; *ir*- inferior rectus; *l*- lashes; *m*- Meibomian glands in tarsus of lid; *n*- nasolacrimal duct; *p*- punctæ lacrimalia; *s*- lacrimal sac; *so*- superior oblique; *sr*- superior rectus; *t*- trochlea (pulley) over which tendon of superior oblique passes.

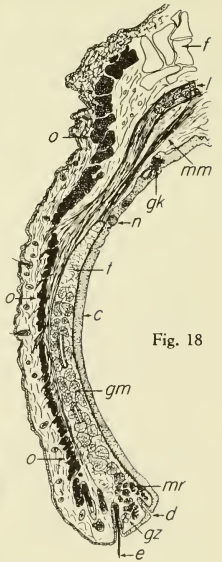

Fig. 18

Fig. 18—Vertical section of human upper lid. From a preparation of K. Lindorfer. *c*- conjunctival lining of lid; *d*- duct of Meibomian gland; *e*- eyelash; *f*- fat; *gk*- accessory lacrimal glandule of Krause; *gm*- gland of Meibom embedded in tarsal plate; *gz*- gland of Zeis (oil-gland of eyelash follicle); *l*- levator muscle (its sheet-like tendon sends slips between fascicles of orbicularis oculi to terminate in dermis of outer skin); *mm*- muscle of Müller (an unstriped slip of the levator, which inserts at upper end of tarsus); *mr*- muscle of Riolan (fine-fibered portion of orbicularis oculi lying behind lash follicles); *n*- lymphatic nodule; *o, o*- orbicularis oculi muscle; *t*- tarsal plate.

therefrom in the embryo and sometimes bears eyelashes and their associated glands as evidence of its true nature.

Near the inner canthus on each lid margin is a pore raised on an eminence. These 'punctæ lacrimalia' are exits for the tear fluid which accumulates in a pool, the lacus lacrimalis, at the inner canthus.

The human upper lid (Fig. 18) does most of the work in closing the eye, though in most vertebrates it is the lower which moves the more. A continuous sphincter muscle surrounds the palpebral fissure and is much flattened and very broad where it courses through the two lids between their outer dermal and inner conjunctival surfaces. The opponents of this 'orbicularis oculi' muscle are thin muscles running down into the upper lid and up into the lower. The more important of these is the levator muscle of the upper lid, which works with the superior rectus of which it is a derivative. Thus, when the eyeball is turned upward the lid automatically rises. When the levator is paralyzed, as sometimes occurs in diseases of the nervous system, the individual has a sleepy look owing to the unsightly drooping of the lid; but the ophthalmic surgeon cleverly corrects this by fastening the inside of the lid to the superior rectus itself.

Between the muscle-sheets of the lids and their conjunctival linings lie firm plates, one in each lid—the tarsi. Each tarsus is composed of dense connective tissue and is curved to fit the surface of the eyeball. Their presence insures a smooth sliding of the lids and obviates any tendency of the latter to roll up when in action. Embedded in each tarsus is a row of elongated (Meibomian) glands which open by a series of apertures behind the lid margin. They represent an additional row of eyelashes which have disappeared in evolution, leaving their glands behind them. The sebaceous secretion of these, together with that of smaller glands (of Zeis) associated with the lashes which are scattered along the edges of the lids, maintains a film of oily emulsion over the layer of tear fluid and holds the latter firmly and smoothly against the eyeball. The tears can spill over onto the cheeks only when they so accumulate that their weight breaks the retaining film.

The periodic blinking of the lids is ordinarily involuntary and unconscious. The rate of blinking varies, but each blink occupies $\frac{1}{40}$ of a second. Its chief values are in moistening and cleaning the cornea and in pumping the tear fluid out of the lacus lacrimalis—though this is an incidental function of the lid muscles rather than of the lids themselves. One might expect the drying of the cornea to initiate the blinking reflex,

but numerous experiments have shown that this is not the case. Though many factors have been tested for their effect or lack of effect upon the acceleration or inhibition of the rhythmical blinking of the lids, the immediate cause of it remains quite unknown.

The Lacrimal System—The tear fluid, which can be thought of as the land animal's substitute for an ocean, is produced continuously in small amounts (less than 1 cc. per day in the absence of irritation) by the lacrimal gland. This compound tubular gland lies against the superior temporal quadrant of the eyeball in the anterior part of the orbit, propped forward by the orbital fat (Fig. 17). Its dozen ducts open mostly far up under the upper lid. Like the lids themselves, the entire lacrimal apparatus is lacking in fishes, where it is not needed, and is much reduced in those aquatic forms which have had terrestrial ancestry. The tears are mixed with mucus secreted by scattered cells in the conjunctiva, and most of this fluid is disposed of by evaporation. Any excess, upon irritation of the eye or in mild emotional states, drains through the two punctæ—chiefly the lower—into a pair of canaliculi which converge and enter the 'lacrimal sac'. This is a dilatation of the upper end of the lacrimal duct, a membranous canal which runs vertically downward, through the bony substance of the skull, to empty into the nasal cavity. This connection leads to our being able to taste the salty tears in the back of the mouth when we weep. There are a number of so-called valves in the tear-drainage system, and its action is rather complicated; but the essential factor in emptying the lacus is a pumping action by the orbicularis oculi upon the adjacent lacrimal sac. This makes it possible to conceal emotion and sometimes to forestall weeping (the spilling of excessive tear fluid onto the cheeks) by rapid blinking.

The primary use of the tears is to clean and wet the cornea. Their overproduction upon irritation is often entirely effective in washing away the source of irritation. The fluid contains enough sugar and protein to be of value in the nutrition of the corneal epithelium, which is able to absorb proteins. There is some evidence that it is the sole source of that nutrition. Moreover, the tears are bactericidal to a not unimportant extent due to the presence in them of a special antiseptic ferment, 'lysozyme'. The most conspicuous thing about the lacrimal system, however, —psychical (emotional) weeping—is strictly peculiar to the human animal and to some species of bears, and serves no physiological purpose whatever. Its value is wholly psychological and economic—as every woman knows!

Chapter 3

THE VERTEBRATE RETINA

(A) Histology and Physiology

The sensory retina of any vertebrate consists essentially of four layers of cells. One of these, the pigment epithelium, is not immediately concerned with the process of photoreception. The other three layers comprise the retina proper, which lies against the pigment epithelium but is rarely connected with the latter by any continuity of material.

The Pigment Epithelium—The pigment epithelium of the retina (Fig. 19) is firmly joined to the inner surface of the chorioid coat. Each cell in the epithelium is like a six-sided tile and the cells are set in a regular mosaic with only a thin layer of cement between their contiguous sides. The base of the cell, toward the chorioid, is also covered by cement which the cell secretes, so that an unbroken layer of this cement lies between the pigment epithelium and the chorioid. The innermost layer of the chorioid is an extremely thin elastic sheet which, together with the cuticular cement layer between it and the bodies of the pigment cells, comprises the 'glass membrane' (lamina vitrea). The whole of the thickness of this really double membrane is often assigned to the chorioid—or, by some, even to the pigment epithelium, which clings much more tightly to the chorioid than to the retina proper when an attempt is made to peel the layers of the eyeball wall apart. The pigment epithelium belongs to the retina physiologically and embryologically, however, if not anatomically. It is nowhere continuous with the chorioid, whereas, as we have seen (see Fig. 7g, p. 15) it is continuous at the pupil margin with the anterior prolongation of the sensory retina.

The free surface of the pigment cell usually bears a number of processes which may be few and heavy (even single) or numerous and filamentous, like a tuft of microscopic hairs (Fig. 20). The granules of pigment, which consist of a colorless matrix impregnated with a light brown form of melanin called 'fuscin', are of two sorts—round ones tending to occupy the cuboidal base of the cell around the nucleus, and spindle-shaped ones filling the processes and often migrating in and out

of the latter in bright and dim light. Pigment may be entirely lacking over a large area of the epithelium where this lies against an especially modified area of chorioid (Chapter 9, section D).

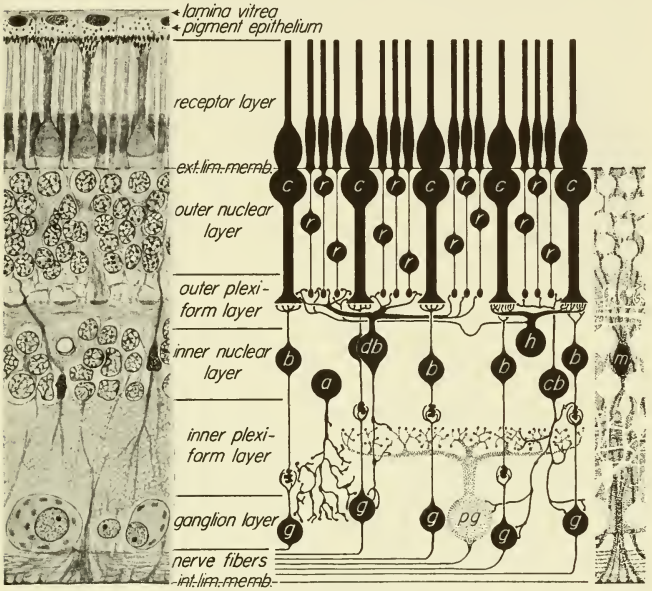

Fig. 19—The human retina.

At the left, a vertical section through the retina in the nasal fundus, as it appears in ordinary histological preparations (fixation in Kolmer's fluid; nitrocellulose embedding; Mallory's triple stain, Heidenhain's hematoxylin and phloxine). × 500. (Note cross-section of capillary in inner nuclear layer).

At the right, a 'wiring diagram' of the retina showing examples of its principal elements, as revealed in material impregnated with silver by the methods of Golgi. Based largely upon the work of Polyak.

a- amacrine cell (diffuse type); *b, b*- bipolar cells (ordinary, 'midget' type); *c, c*- cones; *cb*- 'centrifugal' bipolar, believed by Polyak to conduct outward through the retina rather than inward; *db*- diffuse bipolar, connecting with many visual cells—chiefly rods; *g, g*- ganglion cells (ordinary, 'midget' type); *h*- horizontal cell—its dendrites connecting only with cones and its axon with both rods and cones at some distance from the cell-body; *m*- Müller fiber—its ends forming the limiting membranes and its substance serving to insulate the nervous elements from each other except at synapses; *pg*- 'parasol' ganglion cell (one of several giant types, connecting with many bipolars); *r, r*- rods.

Anterior to the ora terminalis the pigment epithelium passes over the ciliary body as the outermost of the two layers of the ciliary epithelium and is almost unchanged except for an increase in the height of its cells and the disappearance of all processes together with the spindle form of pigment granule. Its continuation on the back of the iris is

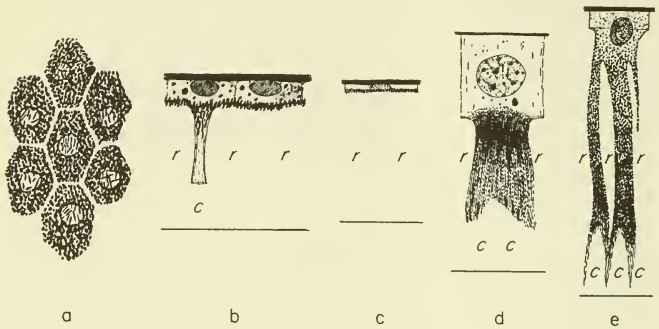

Fig. 20—Pigment-epithelial cells. × 500.

The horizontal line beneath each drawing shows the position of the external limiting membrane. A portion of the lamina vitrea is shown as a heavy black line. Spaces occupied by cones are marked *c;* those filled by rods are marked *r.*

a, group of cells from an unstained, flat mount of human pigment epithelium, as seen from the chorioid side. Through the clearings formed by the nuclei, some of the elongated pigment granules in the distal part of the cell can be seen.

b, two human pigment cells from the nasal periphery, in vertical section. One cell is opposite a cone, and bears a delicate tubular process which ensheathes the cone outer segment (*cf.* Fig. 19). The other cell is opposite only rods, and is devoid of processes.

c, pigment cell of a mouse opossum, *Marmosa mexicana,* showing the paucity of retinal pigment characteristic of many strongly nocturnal animals.

d, pigment cell of an African lungfish, *Protopterus æthiopicus,* showing a mass of filamentous pigment-laden processes markedly differentiated from the body of the cell.

e, pigment cell of goldfish, *Carassius auratus,* light-adapted. The two or three heavy processes contain relatively little migratory pigment (in rod-like granules) in their tips (*cf.* Fig. 62, p. 146; Fig. 94, p. 237).

almost devoid of pigment in those animals in which it has produced a dilatator pupillæ (Fig. 7, p. 15). At the edge of the pupil the layer of cells doubles back upon itself and continues, now heavily pigmented, to the periphery of the iris as the latter's most posterior layer of tissue. There its pigmentation disappears and a clear epithelium proceeds over

the ciliary body, as the innermost of the two layers of the ciliary epithelium, to the ora terminalis. At this point the simple epithelium suddenly becomes stratified and complex to form the sensory retina.

Travelling thus forward to the pupil in the pigment epithelium and backward again into the sensory retina proper, we are easily able to see that the entire retinal coat of the eye reaches to the pupil margin and forms a two-layered cup. The two major layers—pigment epithelium and retina proper—develop directly from the two layers of the embryonic optic cup, which arises as a bubble of tissue on the side of the brain, becoming constricted off therefrom and deeply indented on the side toward the skin. This indentation gives the vesicle an outer and an inner layer and an opening, aimed toward the surface of the head, into which the lens is received after its separation from the skin (see Fig. 38, p. 106). Thereafter the opening becomes (relatively) smaller, and persists as the pupil.

The Visual-Cell Layer—Standing on the external surface of the retina proper, and constituting its receptive layer, are the rods and cones (Fig. 19). These elongated cells thus point away from the light, which must pass through the remainder of the retina to reach them (hence the complete transparency of this tissue as contrasted with the brain, which has a similar histological organization). Their tips are pressed against the pigment cells or are even buried in deep indentations in them, or between their processes when such are present. The processes in turn may reach nearly to the bases of the rods and cones so that they are deeply interdigitated with the latter. Though there is seldom a continuity of substance, the dovetailing of the sets of processes and visual cells is so intimate and firm that one or the other is often torn in two if the retina and chorioid are forcibly separated. In other cases the absence of all pigment-cell processes may make a separation very easy, and only the optic nerve, the fusion of the two layers of the optic cup at the ora terminalis, and the pressure of the vitreous then hold the retina firmly and smoothly in place.

At the level of the bases of the rods and cones the retina has its external limiting membrane (briefly, the 'limitans') which may be likened to a piece of wire screening through each hole of which a rod or cone projects. The visual cells are a tight fit for the holes and are thus kept perpendicular to the membrane and prevented from getting out of line by any sliding lengthwise past each other. In some retinæ, delicate hair-like processes from the outer surface of the membrane itself form so-

called fiber-baskets, fused with the surfaces of the bases of the visual cells and anchoring them very firmly in place.

On the inner side of the limitans lie the nuclei of the rods and cones. The diameters of these are ordinarily much greater than those of the cytoplasmic parts which protrude outward through the limitans. This results in the nuclei piling up into several rows (forming the 'outer nuclear layer') the number of which in a given retina will be roughly equal to the quotient of the square of the diameter of the nucleus divided by the square of the diameter of the predominant type of visual cell. Cones are usually so plump at their bases that there is room for their nuclei to lie up against the limitans or even above it; but a rod nucleus may lie far below its rod, being connected with the latter by a slender thread which winds its way up among the intervening rows of nuclei.

The Bipolar Layer—From each visual-cell nucleus a short thread-like 'foot-piece' travels inward (toward the vitreous) until it clears the other visual-cell nuclei, and then expands into a terminus which may be either smoothly rounded, or branched like a bird's foot (Figs. 19, 22, 23, 24). This is related, as in a handclasp, to a similar arborization at the outer end of a 'bipolar' neuron, whose cell body lies deeper in the retina toward the vitreous. A bipolar dendrite may embrace several or a great many visual-cell termini, so that the number of bipolar cells in a retina is always less than the number of visual cells. The branched process of the bipolar cell which joins to the visual cells, and the similar process from the bipolar cell-body which travels in the opposite direction (toward the vitreous) are however much more slender than the cell-body. The bipolar nuclei are consequently piled up in several layers like those of the visual cells, and this second band of nuclei forms the 'inner nuclear layer' of the retina (Fig. 19). In this layer, along with the nuclei of bipolar cells, are a (usually) smaller number of nuclei belonging to several types of cells which will be mentioned later.

Some of the bipolar cells each connect with but one cone. Such are the numerous 'midget bipolars' of the primate retina (Fig. 19, *b*). Other, 'diffuse' bipolars (Fig. 19, *db*) of several types may each embrace a great number of rods, and some cones as well. In many retinæ there are diffuse bipolars which connect only with rods, or only with cones; but such elements appear to be lacking in man.

The inner nuclear layer is separated from the outer nuclear layer by a feltwork of the delicate nerve fibers which make the connections

between visual cells and bipolars. This is the 'outer plexiform layer'. An 'inner plexiform layer' also occurs on the vitread side of the inner nuclear layer, and has a similar significance. In it lie the synaptic junctions between bipolar cells and the innermost of the three masses of cells concerned with the projection of the image to the brain—the 'ganglion layer'.

The Ganglion Layer—The cells of this layer (Fig. 19) have either small or large bodies and simple or elaborate dendrites which reach up into the inner plexiform layer to meet the termini of the bipolars. Each ganglion cell gives off a slender axon process which courses along the inner surface of the retina, next to the vitreous. All of these fibers, from

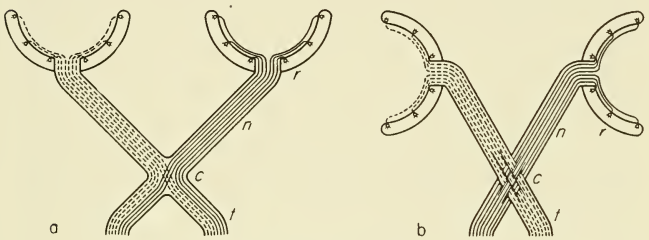

Fig. 21—The optic chiasma.

a, of man, showing partial decussation of optic nerve fibers.

b, of bird, showing total decussation; in some vertebrates (*i.e.*, most fishes) the nerves are not thus plaited—but whether the fibers are interwoven or not, they all decussate in non-mammals.

c- chiasma; *n*- optic nerve; *r*- retina; *t*- optic tract, which enters brain.

all over the sensory retina, converge at one place in the 'fundus' (back) of the eye and there turn parallel to each other and pass outward through the retina, chorioid and sclera in a compact bundle as the optic nerve, which travels toward the brain (Fig. 21).

A ganglion cell may gather in the axons of several bipolars (Fig. 19, *pg*), just as one of the latter in turn often connects not with one visual cell but with several. This has been called the 'inward convergence' of the visual cells upon optic nerve fibers, or 'summation'. The impulses which travel down several visual-cell foot-pieces are *summated* in their efforts to stimulate a single bipolar cell, and numbers of bipolar nerve-impulses are in turn gathered into single ganglion cells and optic nerve

fibers. This phenomenon of summation is of the utmost importance in the physiology of the retina, and will be discussed again when certain other concepts have been introduced.

The three kinds of retinal elements so far mentioned—visual, bipolar, and ganglion cells—are those concerned in the simple, straightforward, projective pathway of the visual impulse to the brain. There are four other types of cells which remain to be described: Müller fibers, neuroglial cells, horizontal cells, and amacrine cells.

Müller Fibers—Müller fibers may be likened to rivets which run through the whole thickness of the retina proper and bind its layers together (Fig. 19, *m*). Their outer ends form the external limitans and their inner ends are expanded into trumpets or pyramids whose bases, against the vitreous, are six-sided and are fitted together as an unbroken mosaic, the internal limiting membrane of the retina. This is not a true, isolable membrane but simply the inner surface of the retina. The vitreous which touches the internal limitans may be a little tougher than the rest, like the skin on a cornstarch pudding; but it is still part of the vitreous—there is no distinct layer at the retino-vitreal interface which belongs to neither structure. The retina and vitreous are simply in contact.

The nucleus of a Müller fiber lies about half-way through the thickness of the inner nuclear layer and is very easily identified by its elongated oval form. The boundary surface of a Müller fiber, however, cannot be made out at all unless the cell is isolated by the procedure of macerating the retina; for the Müller fibers have irregular expansions and cavities in them, and occupy a surprising amount of the total volume of the retina. If we imagine building a model of the retina by using wires for the nerve fibers in it, and large glass beads for their nuclei, we could then represent the whole population of Müller fibers best by filling in all the empty space with wax or some such substance. All of the nuclei in the retina sit in pockets in the Müller fibers, which at the levels of the nuclear layers form a sort of sponge-work. Every nerve-fiber is likewise insulated from every other by a film of intervening Müller-fiber substance; and only at the synaptic handclasps between nerve-fiber ends is there opportunity for separate nerve cells actually to come in direct contact.

Neuroglia—The neuroglial cells of the retina are small and not numerous. They are like one of the chief types of glial elements in the brain and spinal cord. While glial cells are abundant and important in serving

as the connective-tissue of the central nervous system, their place is taken in the retina by the Müller fibers, which do the same job even better and other jobs in addition. We may fairly consider the glial cells of the retina to be meaningless, and present only because of their inheritance from the brain wall of which the retina is, after all, a part. Occasionally they seem to resent their idleness and become altogether too busy, generating a 'glioma'—a particularly disastrous type of tumor whose presence calls for the immediate removal of the eye to prevent a fatal involvement of the brain by way of the optic nerve.

Horizontal and Amacrine Cells—Although the Müller fibers and neuroglial cells are certainly not impulse-conducting elements, the 'horizontal cells' are under suspicion of performing some sort of integration of the retina. If we think of the visual→bipolar→ganglion-cell chain as running *vertically* through the retina, then the amacrines and horizontal cells do their work in a *horizontal* direction. The horizontals have their cell-bodies among those at the outer surface of the inner nuclear layer (Fig. 19, *h*). In lower vertebrates the horizontal cells are chunky and epithelioid, or ropy and anucleate, and seem only to have a supporting function like the Müller fibers. In higher vertebrates, however, they more often have many spider-leg processes running in the outer plexiform layer. Thus they may give the appearance of nerve cells and very probably do conduct laterally, tying up one area of the retina with another just as regions of the cerebral cortex are interconnected by association fibers. Those of mammals (Fig. 19, *h*) are certainly conductive, and in man have their stubby dendrites connected with cones and their long axons connected with distant rods and cones.

The 'amacrine' cells ordinarily have this same horizontally integrative function. Their exact action and its effects upon subjective visual phenomena are about the biggest remaining mystery in the physiology of the retina. Their nuclei tend to lie in the inner half of the inner nuclear layer and each gives off a single process which passes vitread and then branches more or less, the branches being short or very long (Fig. 19, *a*). The amacrines seem to associate the bipolar→ganglion-cell synapses, performing for the inner plexiform layer the same function that the conductive types of horizontal cells do for the outer.

The action of these two types of cells would *appear* to be detrimental to the preservation of the pattern of the retinal image during its 'wirephoto' transmission to the brain in the form of nerve-impulses. If all the

amacrines were carrying impulses at once, the result would certainly be a hopeless garbling of the projective transmission and a blurring of the cerebral picture of the external visual field. One would, then, expect to find amacrines very few or even lacking in the retinæ of those animals whose vision is keenest and whose ability to discriminate fine-detailed patterns is greatest. Yet it is in just such animals that the amacrines are most abundant. In the birds, for example, they may even outnumber the bipolar neurons. Obviously, only a few can be in action at any one time, and they make of the retina an elaborate switchboard in which now one, now another conduction may be enhanced or inhibited.

In primates, some of the elements formerly believed to be 'amacrine' (literally, 'lacking an axon') have recently been found to possess axons after all. If their axons and dendrites have indeed been correctly identified (and the identifications are so far on a purely morphological basis), then such elements are really bipolars of a peculiar sort—they conduct *toward* the receptor layer. Such a supposed 'centrifugal' bipolar is shown in Figure 19 (*cb*). Their discoverer, Polyak, thinks that they serve to alter the state of activity of the visual cells. What this may mean, translated into terms of visual physiology and visual psychology, is not clear. It seems as likely that the centrifugal bipolars intensify (or prolong) the activity of ordinary bipolars in a given amount or pattern of illumination, by (so to say) taking excitation from their lower ends and putting it back in at their tops. Anyone familiar with radio hook-ups (which the diagram in Fig. 19 rather resembles!) can see how the centrifugal bipolar may be compared with a tickler coil in a regenerative circuit.

There are many true amacrines in primates, however; and these axonless, horizontal integrators are abundant in other vertebrates—particularly so, in birds (*v. s.*).

A moment's thought about the mystery of the amacrines suffices to convince one that the retina is more than just a sense organ which retails to the brain, parrot-fashion, the physical changes in the environment. The retina is an association center with every bit as complex a mode of action as the cerebral cortex itself. The elucidation of its switchboard activities is almost beyond the realm of physiology.

Nutrition of the Retina—The nervous tissue of the retina probably does not have a high rate of metabolism, but the rods and cones are very sensitive to any interference with their supplies of materials and oxygen. These come from the chorioid, which aside from its light-absorbing func-

tion is wholly devoted to the nutrition of the visual cells. The turnover of substances must be very great, for the chorioid is very rich in blood vessels which indeed comprise most of its bulk in many animals.

Just outside of the lamina vitrea lies a network composed of broad, flat capillaries. This 'choriocapillaris' reticulum (Fig. 6b, p. 14) is so fine-meshed that its capillaries total a greater portion of its area than do the spaces between them. It is with the blood in the choriocapillaris that the visual cells make their exchanges of supplies and wastes, liaison being effected by the pigment epithelium which is thus taking in and giving off materials at both of its surfaces continuously. The retina often has blood vessels clinging to or embedded in its inner surface, but these are usually concerned only with the nutrition of the inner layers of the retina. Even where (as in most mammals) capillary branches of these vessels invade the retina itself, they almost never reach outward beyond the inner nuclear layer and obviously belong only to the vitread portion of the retina. Such a capillary shows in Figure 19.

The choriocapillaris is supplied with blood by a layer of arteries outside of it in the chorioid, and drains into a layer of large inter-connecting veins which lie on the scleral side of these arteries (Figs. 4a, 6a; pp. 8, 14). The veins converge in the four quadrants of the eyeball to pour their contents into the four great 'vorticose veins' which conduct the blood away from the equator of the eye. Other vessels also penetrate the sclera anteriorly and supply or drain structures other than the retina. The vessels mentioned above, which supply the inner layers of the retina, are few and are branches of vessels which enter the eyeball in or along with the optic nerve. True retinal vessels are present only in the eels and the mammals—and not even in all of the latter, some of whose retinæ (*e.g.*, in the rhinoceros) are as completely avascular as those of the lower vertebrates.

All of the vessels concerned with the eye apart from the retina—and even including those last mentioned above—do not, taken together, compare in abundance with the rich chorioidal circulation. This latter exists solely for the benefit of those cells of the whole eye which are most important, if any are that: the rod and cone visual cells.

The Optic Nerve—The human optic nerve takes a long, slightly undulant course to the apex of the orbit and there enters the cranium (Fig. 16, p. 37). It is flexible, and by its length allows enough slack to let the eye rotate freely. It contains more than a million nerve fibers, most of

which transmit visual impulses, though many are centrifugal. It is heavily ensheathed by tendinous and vascular coats continuous on the one hand with the sclera and on the other hand with the meningeal coverings of the brain, and is divided by internal septa, of connective tissue and neuroglia, into many fiber-bundles. The central retinal artery and vein join the nerve at some distance from the eyeball and run through its center to emerge within the eye at the nerve head, where they branch over the inner surface of the retina. The optic 'nerve' is called such only for convenience. It is not a true nerve but, like the retina, an ectopic portion of the brain itself.

Within the cranium the two optic nerves cross through each other and continue, as the 'optic tracts', into the brain. The crossing or 'chiasma' is especially complex in man and in all other mammals, for in them only some of the fibers from each eye cross into the opposite optic tract, the others going directly into the tract on the same side. In other vertebrates, the crossing or 'decussation' of the fibers is complete—that is, all of the fibers from each optic nerve enter the opposite side of the brain (Fig. 21). No special advantage is gained by such an arrangement—it arose mysteriously along with the numerous similar decussations in the tracts of the brain, brain stem, and spinal cord; but there is a special value of *partial* decussation which will be found explained in Chapter 10, section D. Even where the decussation is total, the chiasma is seldom a simple anatomical crossing of one whole optic nerve over the other. This is indeed the situation in most fishes; but elsewhere the two nerves are interwoven to a greater or lesser extent (Fig. 21b).

(B) Types of Visual Cells

General Types–Rods versus Cones—The visual cells of vertebrates are of two general types which were long ago given the names 'rod' and 'cone'—though with our superior modern knowledge of their phylogenetic ramifications and physiological characteristics we might wish that a more apt pair of names could be substituted for the traditional ones. In a given retina containing both highly sensitive visual cells (rods) and relatively insensitive ones (cones), the high- and low-threshold cells can always be told apart; but the rod of one retina may resemble structurally the cone of another, or may give evidence of having been recently

derived from a cone-type in an ancestor of different habits. In an attempt to resolve the confusion resulting from an overemphasis of shape-differences—which has even led some to deny any distinction between rods and cones!—the writer several years ago proposed the names 'photocyte' and 'scotocyte' for the two physiological types of visual cells contrasted in the Duplicity Theory (see next Section). But it is perhaps too late to bring about any such revolution in the terminology.

Of the two types, there can be no doubt that the cone is the older and more primitive. This statement however—which is quite contradictory to any the reader will find in other books—is not to be taken to mean that cones entirely like those of man were the original vertebrate visual cells. It is certain, for instance, that the ancestral cell lacked any means of analyzing colors. It is equally certain that the common ancestor of present-day rods and cones lacked any such ingenious sensitizing substance as rhodopsin (see Chapter 4). With a slender, pointed, stimulable organelle, the outer segment, derived from a formerly vibratile flagellum (see Chapter 5, section B) and connecting directly to a simple afferent neuron, the pro-vertebrate visual cell could not but have been a high-threshold receptor, which limited the excursions of its owner to the brightly lighted surface waters.

Rods came later, as a means of extending the period of activity over a greater portion of the twenty-four hours. They were derived quite simply from cones by the enlargement of the outer segment and by an increase in the number of visual cells connected to each nerve cell. It was not desirable for all of the visual cells to make these changes, for unless two types were preserved side by side in a nice balance, sensitivity to dim light could not be increased without too great a sacrifice of resolving power. The needs of the animal—whether greater for sensitivity, or for visual acuity—then determined the proportion of small un-summated and larger, summated visual cells which would give him optimal visual capacity. With the invention of the powerfully sensitizing rhodopsin by the rod on the one hand, and the differentiation of a photochemical basis for hue-discrimination in the cones on the other hand, the widely useful duplex retina as we know it today came into being.

Single Cones—Because of the antiquity and priority of the high-threshold cell, we will consider first the cytology of a typical single cone such as that of the frog (Fig. 22c). The elaborate cytoplasmic portion of this complex cell protrudes through a lacuna of the external limiting mem-

brane, which constricts its base firmly and keeps the nucleus of the cone on the vitread side. The tapered photosensitive tip of the cell is the outer segment, the remainder of the cell down to the nucleus being the inner segment and representing the columnar body of the ancestral epithelioid ependymal cell. In the distal end of the inner segment lies the

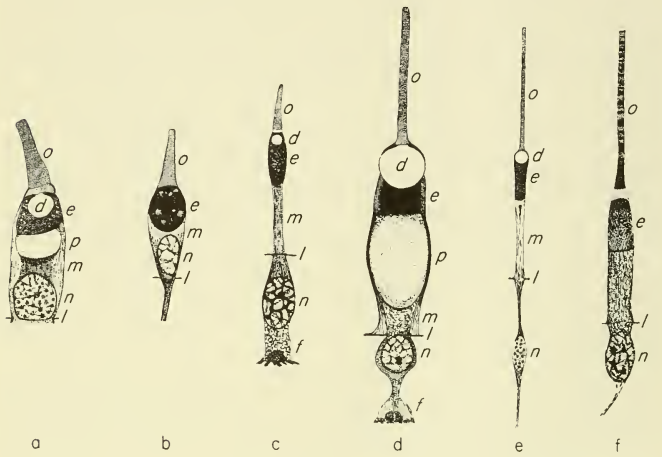

Fig. 22—Single cones. × 1000.

a, of sturgeon, *Acipenser fulvescens*. b, of goldfish, *Carassius auratus;* light-adapted (*i.e.*, with myoid contracted—*cf*. Fig. 62, p. 146; in fishes, the cone nucleus often lies partly or wholly above the external limiting membrane, as here). c, of leopard frog, *Rana pipiens;* dark-adapted (*i.e.*, with myoid elongated—*cf*. Fig. 64, p. 148). d, of snapping turtle, *Chelydra serpentina*. e, of marsh hawk, *Circus hudsonius;* from the circumfoveal eminence. f, of man; from the circumfoveal eminence.

d- oil-droplet, embedded in: *e*- ellipsoid; *f*- foot-piece; *l*- external limiting membrane; *m*- myoid; *n*- nucleus; *o*- outer segment; *p*- paraboloid.

ellipsoid, whose shape in the frog cone happens to justify this geometrical name, though this is seldom true. Embedded distally in the ellipsoid is the oil-droplet, which in some frog cones contains a dissolved yellow pigment. The stalk-like portion of the inner segment is highly contractile (Chapter 7, section B) and hence is called the myoid (= muscle-like). The myoid joins the large, ovoid nucleus in which the chromatin

occurs in a reticulum of many small granules. From the region of the nucleus a short, thick, dendritic 'cone-foot' proceeds vitread to make a synapse-like junction with a bipolar dendrite.

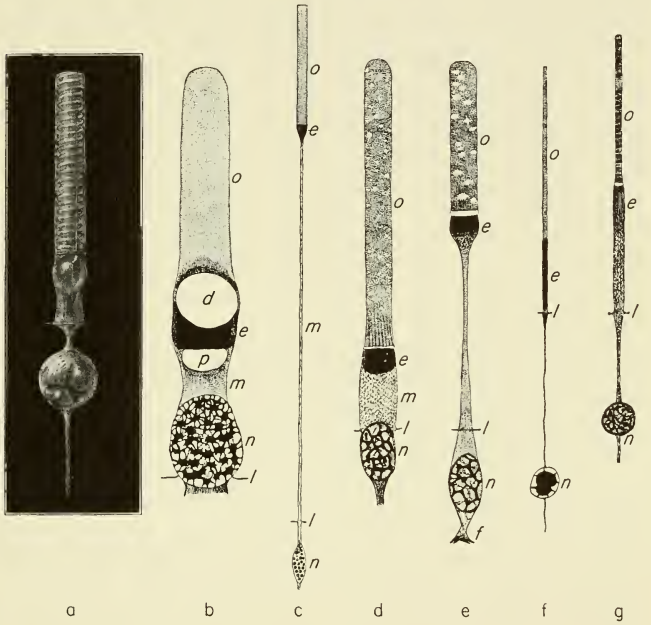

Fig. 23—Rods. × 1000.

a, generalized rod, showing organelles as they might appear if visible in the living cell; note myeloidal spiral and centrosomic Fürst fiber in outer segment, diplosome and Kolmer-Held fiber proceeding therefrom in inner segment. b, rod of *Protopterus æthiopicus*—unusual, in that it contains an oil-droplet, implying secondary origin from a cone (*cf.* Fig. 25). c, rod of goldfish, *Carassius auratus;* light-adapted (*i.e.,* with myoid elongated—*cf.* Figs. 62 and 63). d, common or 'red' (rhodopsin-containing) rod of leopard frog, *Rana pipiens;* dark-adapted (*i.e.,* with myoid contracted—*cf.* Fig. 64). e, 'green' (Schwalbe's) rod of *Rana pipiens.* f, rod of flying squirrel, *Glaucomys v. volans;* exemplifies the filamentous type characteristic of many strongly nocturnal animals. g, human rod from near the temporal side of the macula lutea.

d, oil-droplet; *e-* ellipsoid; *f-* foot-piece; *l-* external limiting membrane; *m-* myoid (the corresponding portion of the inner segment is non-contractile in e, f, and g); *n-* nucleus; *o-* outer segment; *p-* paraboloid.

Not all single cones are built like those of the frog. The oil-droplet is lacking in the cones of nearly all living forms lower than the frogs; but even so there are reasons for thinking the oil-droplet to be a very primitive visual-cell feature. Such droplets occur in pigment epithelial cells, which are homologous with the visual cells, and apparently also (in salamanders) in the type of brain-cell from which the rods and cones originated. The ellipsoid, which appears to be a light-concentrating device, is sometimes supplemented by a second dioptric organelle, the paraboloid, lying proximal to it in the myoid. The paraboloid may have some very important function other than its incidental optical one. While the ellipsoid always stains heavily with acid fuchsin, an outstanding peculiarity of the paraboloid is its usual refusal to take any stains at all. It is quite likely that some paraboloids are fluid vacuoles—perhaps sometimes artificial spaces (Figs. 22a, 23b, 24a and b); but many are solid or semisolid (Figs. 22d, 25) and keep their shape when expressed from the living cell.

The cone outer segment may actually be cylindrical when it is so very slender that it could hardly be expected to taper, as in many lizards and birds, and even sometimes when there is plenty of room for a more bulky, conical structure (Fig. 22). The myoid may be quite non-contractile and thus undeserving of that name, as in man; and it may be permanently greatly elongated, marooning the body of the cone opposite or even beyond the tips of the rods (flying squirrels, some lampreys and snakes—see Fig. 69a, p. 167). The nucleus of the frog cone is typical structurally, but not as regards its position, for cone nuclei almost always lie in contact with the limitans or even (some fishes) beyond it, on its scleral surface (Fig. 22a and b).

One of the most noteworthy peculiarities which cones may have is that presented by the cones of the greater portion of the human retina, and also by some other placental mammals, the dog and cat for example: the cone outer segment is a cylinder enclosed by a tubular process of the pigment epithelial cell opposite to it, and apparently (though this is not yet certain) fused at its tip with the pigment cell, actual protoplasmic continuity existing between the two (Figs. 19, 20b; pp. 43, 44). No such arrangement is ever seen in rods, and its obvious advantages for the facilitation of the nutrition of the cone constitute important evidence for the cone's having a faster metabolism than the rod—something which has long been suspected on other grounds.

Rods—One rod would do about as well as another to illustrate rod structure, for rods do not differ from retina to retina nearly so much as do cones. The rod (Fig. 23) has the same principal parts as the cone —outer and inner segments, nucleus, and foot-piece. The outer segment is almost without exception a perfect cylinder and the inner segment is often more slender—sometimes, as in bony fishes, much more so.

The rod in man and other mammals is not contractile; so, the term 'myoid' for the undifferentiated part of the inner segment would be a misnomer. A structure corresponding in microchemical behavior to the cone ellipsoid is present, though it is probably optically functionless. Rod nuclei tend to be smaller, more nearly spherical, and with much larger and fewer masses of chromatin than cone nuclei. The latter having preëmpted positions against the limitans (the cones being the first visual cells to differentiate in embryonic retinæ), the rod nuclei perforce contact the limitans only between cone nuclei and for the most part are forced to pile up below it to form the thick outer nuclear layer.

Cones ordinarily vary considerably in different retinal regions, being more slender and more numerous toward the fundus. Rods are uniform in concentration everywhere except as this is influenced by the cones—it is as though the cones had been distributed in the retina first, and then the spaces between them neatly filled in with as many rods as would conveniently fit. Rods are ordinarily uniform in diameter throughout a retina, but their length tends to increase slightly and slowly from ora to fundus. The center of concentration of cones, or of rods when they have such a center, does not necessarily lie anywhere near the optic axis of the eye. Seen 'on the flat', the rod and cone mosaic exhibits a pattern which in different animals may have the hexagon, the square, or some other geometrical figure as its unit. These patterns have not yet been sufficiently studied for them to yield up any ulterior meaning which they may have.

Homology of Rods and Cones—Cone and rod are homologous part for part and have many points in common. The outer segments of both have thin sheaths filled up with a lipid ground-substance in which one or more closely wound spiral filaments of another lipid material, derived from mitochondria, are embedded (Fig. 23a). These show faintly or clearly in large rod outer segments (Figs. 25 and 26), rarely also in cones; but they are presumably always present. When too heavily stained, they commonly give an appearance of transverse discs (Figs.

22f, 23g). A long filament runs axially or peripherally in the outer segment of (again, presumably) every visual cell and, just within the inner segment, is connected with a pair of granules from which a second, much shorter, filament proceeds down the inner segment for a way (Fig. 23a). This filament-and-granule apparatus, collectively, is the centrosome of the cell, whose function in visual physiology, if any, is not known. Rods may contain paraboloids, or even oil-droplets (Figs. 23b, 25b, c), though only when the rods have had a peculiar history (Chapter 7, section D). The rod foot-piece may be just like a cone-foot; but in animals whose rods are very slender and numerous (teleosts, mammals, and nocturnal birds) it is a slender filament terminating in a highly specialized, unbranched 'rod end-knob'—apparently to make more compact the connections of many rods to single bipolars (Fig. 19, p. 43).

It is also in such animals that the rod and cone nuclei are most sharply differentiated as to size, shape, and chromatin distribution. In forms with fewer, more bulky rods (lampreys, amphibians, many reptiles) the rod and cone nuclei are indistinguishable on any basis other than position, and the foot-pieces may be nearly or quite identical. In connection with the question whether the rod or the cone is the more primitive cell, it is significant that when the nuclei and foot-pieces are alike in a retina, they both resemble the *cone* structures of retinæ in which they differ—and, cone-type nuclei are more like nuclei in general than are rod-type nuclei. The heavy, dendritic cone-foot would also appear to be a more primitive sort of connecting process than the peculiar rod-fiber and its end-knob. Where they are markedly differentiated, the differences between rod and cone nuclei have no relationship to physiological differences which we are able to discern at present.

Green Rods—There is a type of so-called rod, restricted to the amphibians, whose very long stalk is but slightly contractile (Fig. 23e). It lacks rhodopsin and this, together with the shortness of its outer segment, would necessarily make it have a relatively high threshold. Functionally, this 'green rod' (of Schwalbe) is probably more cone-like than rod-like—its nucleus even lies in the inner part of the outer nuclear layer, alongside the cone nuclei; but its origin is quite unknown.

Double Cones—Even more mysterious are the 'double cones'—and the puzzle they present is particularly irritating to the curious investigator because they are so very widespread among vertebrates. If they occurred in only one or two animals, we might dismiss them as a curi-

osity. Perhaps if they occurred in the human retina we would before now have gained some clue to their rôle in visual processes; but their functional significance, their exact mode of formation in the developing retina, and the probable time and manner of their evolutionary origin have yet to be determined. Next to the amacrine cells, the double cones

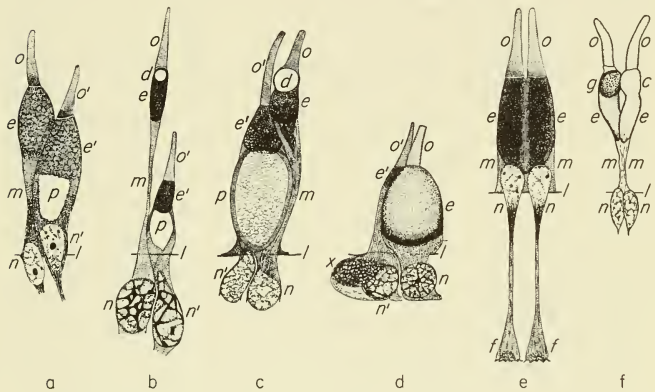

Fig. 24—Double and twin cones. × 1000.

a, double cone of a holostean fish, the bowfin, *Amia calva.* **b**, double cone of leopard frog, *Rana pipiens;* dark-adapted (*i.e.,* with myoid of chief cone elongated). **c**, double cone of western painted turtle, *Chrysemys picta marginata.* **d**, double cone of European grass snake, *Natrix natrix.* **e**, twin cone of a teleost fish, the bluegill, *Lepomis m. macrochirus;* light-adapted (*i.e.,* with fused myoids contracted). **f**, conjugate element (of *Fundulus heteroclitus;* after Butcher) characteristic of some teleosts; perhaps intermediate between **a** and **e**, perhaps instead a derivative of **e**.

c- 'clear mass'; *d*- oil-droplet; *e*- ellipsoid of chief cone; *e'*- ellipsoid of accessory cone; *f*- foot-piece; *g*- 'granular mass'; *l*- external limiting membrane; *m*- myoid; *n*- nucleus of chief; *n'*- nucleus of accessory; *o*- outer segment of chief; *o'*- outer segment of accessory; *p*- paraboloid.

are physiologically the most obscure elements in any and all retinæ. They have unfortunately not greatly interested visual physiologists, since the latter have their attention focused upon the human retina, in which double cones are lacking.

Double cones appear phylogenetically first in the holostean fishes (Fig. 24a). They occur in amphibians, reptiles, birds, one monotreme (*Ornithorhynchus*) and marsupials, but not in any known placental

mammals although some of the most primitive of these may prove to have them when examined. So, most vertebrate groups have double cones; yet we have no idea what they mean. The most that can be said is that the number of double cones, relative to the total number of cones, tends to be high in strongly diurnal animals and low in strongly nocturnal ones. As a maximum, double cones may about equal in number the single cones of the same retina.

The typical double cone (Fig. 24b, c) consists of two very unlike cones fused together in the lower myoid region. One member—the chief cone—is always very much like the single cones in the same retina. The other, or accessory cone is decidedly different. The ellipsoid is usually unclear in outline proximally and its material blends with the ground substance of the inner segment. There is almost never an oil-droplet, but an enormous paraboloid is almost invariably present. This so distends the accessory myoid that the myoid of the chief cone is thinned and curved around the paraboloid region so as to be almost indistinguishable proximally. There are two nuclei, and some indications that the two foot-pieces connect with different bipolars. The two members of a double cone seem to supplement each other—an organelle which one lacks, the other possesses; but since everything that may be present in the two members together may also occur in one single cone, the segregation of parts in the double cone is without obvious meaning.

Twin Cones—Quite another sort of element is the 'twin cone' (Fig. 24e) found in so many teleost fishes. In this receptor the two members are identical and are fused throughout the length of the inner segment. Thus the twinned myoid contracts and elongates as a unit during photomechanical changes, whereas in double cones only the chief member moves, the accessory having no myoid in the proper sense of the word.

Twin cones are strictly a teleostean monopoly. These fishes being a terminal group in evolution, it is impossible to believe that ordinary double cones developed from twin cones; nor is there much reason to suppose that twin cones were ever double ones of the type described above. But there are elements in some teleosts which for want of a third possible name we shall have to call double cones (Fig. 24f). They seem to represent twin cones in which the two ellipsoids and outer segments have become unequal in size and different in staining properties and hence, chemico-physical makeup; but the zone of fusion still extends the whole length of the inner segment so that the two myoids contract and

lengthen as one. These structures indicate that the makeup of the common double cone is worth imitating for some reason; and we shall see shortly that the snakes have also discovered this for themselves. But, until the distribution of these peculiar elements is better known and has been related to teleostean taxonomy, there remains the possibility that some of them are derivatives of holostean double cones (Fig. 24a) which have never quite equalized their two members, rather than a secondary departure of twin cones in the direction of double ones.

Like the double cones of other classes, the twin cones of the teleosts appear to be related to diurnal activity. Wunder has shown that they are most numerous in surface fishes, less and less common in fishes which habitually swim at greater and greater depths. Thus they seem somehow to be associated with vision in bright light, though apparently not with sharp vision since they are excluded from teleost foveæ. More than that cannot be said about them in the light of present knowledge.

Ophidian Double Cones—The double cones of snakes are quite unique. Though all lizards have double elements of the standard type (Fig. 25a), the primitive snakes of the boa family have only single cones of one kind, together with rods (Fig. 69b, p. 167). In the big central family of snakes, the Colubridæ, the standard retina contains only cones of three types. One of these (Type A) is a large single cone and is abundant. Another (Type C) is a small single cone which occurs always in small numbers and is entirely lacking in the retinæ whose resolving power is highest.

The Type B, double, cone (Fig. 24d) bears no resemblance to double cones outside the snakes. Its chief member is bulky, and is identical with the Type A single cone. The accessory is extremely slender and is fused with the chief cone throughout the length of the inner segment. The accessory nucleus is often displaced laterally in the outer nuclear layer; and applied to it is an organelle, the paranuclear body, which occurs only in ophidian double visual cells. Snake cones have no oil-droplets or paraboloids, and the ellipsoid usually fails to stain with acid fuchsin. The inversion of size-relationship of chief and accessory, the paranuclear body, the absence of a paraboloid, and the extensive fusion of the inner segments set the ophidian double cone off so sharply from all others that even if it were present in the Boidæ one could feel certain that it was originated *de novo* within the snake group, and represents the second—at least—separate invention of a double cone by vertebrates.

Double Rods—Still another kind of visual cell is the double rod. These were long known in geckoes (a family of nocturnal lizards) and have recently been found in snakes. The gecko double rod (Fig. 25) was

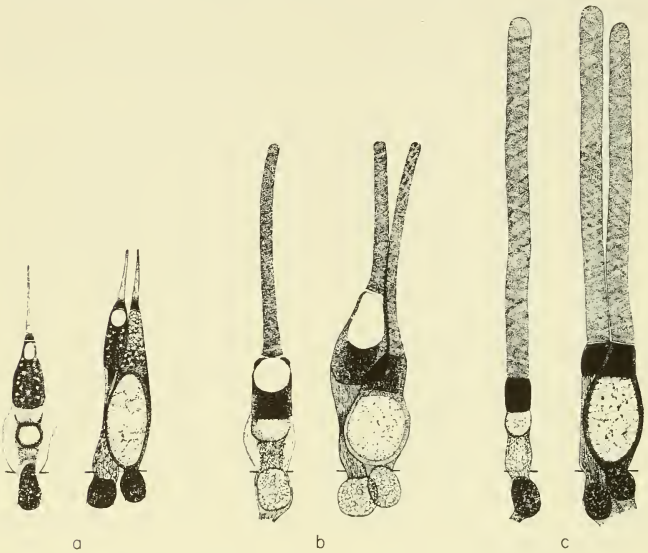

Fig. 25—Double rods in lizards, and their derivation. × 1000.

a, the two cell-types of the pure-cone retina of the (diurnal) collared lizard, *Crotaphytus collaris;* parts as in Figs. 22 and 24. The outer segments are tiny and the oil-droplet is yellow in life.

b, cell-types of Rivers' night lizard, *Xantusia riversiana.* The outer segments have become rod-like but contain no rhodopsin, and the oil-droplets are large and colorless. Morphologically, these elements are intermediate between cones and rods; physiologically, they are low-threshold.

c, the cell-types (single and double rods) of the banded gecko, *Coleonyx variegatus.* The massive outer segments contain rhodopsin, and the oil-droplets have disappeared.

certainly not derived from a bifurcated single rod, but directly from a double cone. It is thus closely homologous with the ordinary type of double cone since it is the latter which occurs in diurnal lizards. The double rods in certain snakes (Fig. 26) were just as certainly derived from the peculiar ophidian type of double cone, for they have exactly

the same structure except for the size and shape of the outer segments. They contain no rhodopsin, and owe their sensitivity to the large volume of their outer segments and to their multiple connections to single nerve cells. The gecko double rod does contain a rhodopsin, indicating that this substance, like other pigments such as hemoglobin and melanin, can be evolved repeatedly and was not invented once and for all.

This whole matter of the conversion of one type of visual cell into another will be discussed at some length later (Chapter 7, section D). It has a considerable bearing upon the ability of animal species to change their characteristic behavior with respect to light, and upon the question of the capacity of animals for discriminating colors (see Chapter 12).

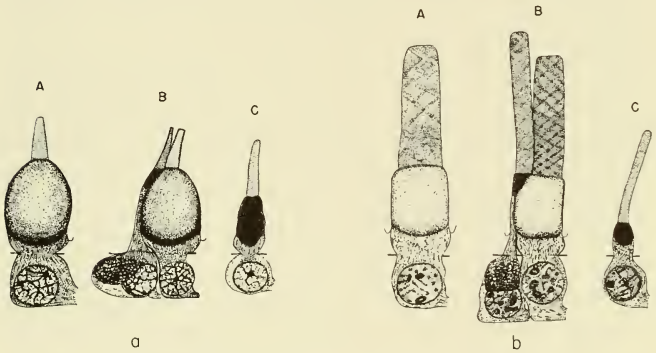

Fig. 26—Double rods in snakes, and their ancestry. × 1000.

a, the three cell-types of the pure-cone retina of a diurnal colubrid, the European grass snake, *Natrix natrix;* parts as in Figs. 22b and 24d. Type A is the ordinary single cone; type B is the double cone, equal in numbers to A; type C is an uncommon single cone with dark-staining ellipsoid.

b, the homologous rod types of the spotted night snake, *Hypsiglena o. ochrorhynchus.* In this genus and in some other colubrids, the ancestral cones have all been converted into rods, through intermediate conditions shown by such forms as *Cemophora, Arizona, Rhinocheilus,* and *Trimorphodon.* See Figure 68a, p. 166.

Since cones can and do change into rods in evolution—and rods into cones, as well, though less often—it is not surprising that numerous halfway stages in such derivations occur in living forms. These are, of course, grist to the mill of those few who insist that any distinction between rods and cones is wholly artificial. Naturally, such cells do defy classification, and will not be considered here as discrete types.

(C) The Duplicity Theory

History—In 1866 the great retinologist Max Schultze unobtrusively announced a conclusion to which he had come after some fifteen years of investigations in comparative ocular histology. He had been struck by the correlation between the relative numbers of rods and cones in various retinæ and the habits of their possessors with regard to light. Nocturnal vertebrates had many rods, and few cones or even none. Diurnal species had many cones, and might even lack rods entirely. Schultze suggested that the cone is the receptor for photopic (bright-light) vision and that the rod is the organ of scotopic (dim-light) vision. To this he added a corollary hypothesis that the cone alone is responsible for color vision; for in dim light colors are no longer discriminable and the world presents itself only in shades of gray.

This theory passed unnoticed by the physiologists and early psychologists until, toward the end of the century, the same idea was brought forward independently by two men who were led to conceive it by different lines of evidence, and neither of whom knew much of Schultze's work. Parinaud, studying human vision in certain pathological conditions, produced his 'théorie des deux rétines'. Von Kries, repeating and extending Schultze's observations on twilight vision, with special reference to the vision of the retinal center, formulated the 'Duplizitätstheorie' about as we have it at present.

It is not at all uncommon for psychologists and medical men to say even today that the Duplicity Theory is "*only* a theory," and to express considerable doubt as to its validity. This ordinarily implies a confinement of knowledge to the basis of the theory in human vision. Of course, if one considers only the known facts of human vision, one cannot expect to be able legitimately to use very many of them to prove the very theory which was evolved to explain them. But the comparative-ophthalmological findings of Schultze and of many zoölogists since his time have built so unshakable a foundation for the theory that its major tenets may be regarded as proven facts. True, there are prominent French retinologists who do not believe in it, but their methods of study are so antiquated that it is hardly surprising that they are unsure of the distinctness of rods and cones.

It is necessary however to bear in mind that the Duplicity Theory as we state it nowadays is really two theories in one. It states that the rods are responsible for the hazy, crude, achromatic (black-gray-white) per-

cepts of dim light and that the cones yield the sharp, detailed images and the chromatic (colored) sensations characteristic of bright-light vision. Actually, the factors which make rod vision unsharp but sensitive, and make cone vision sharp but requiring higher intensities of illumination, are not the same as those which make rod vision achromatic and cone vision chromatic. We may be quite sure that animals with rod-rich or pure-rod retinæ have only diffuse mental pictures and can see in very weak light, but we have at present no proof that all cones are hue-discriminatory and that all rods are not. To date, no animal positively known to have only rods in its retina has been properly tested for color-vision capacity, and many animals which have plenty of cones have been shown *not* to have color vision (see Chapter 12, section A).

Sensitivity versus Acuity—When we say that an animal sees well or sees poorly, that it can see in the dark or that it is blind in the daytime, we are loosely jumbling together two aspects of vision which should be carefully distinguished and thoroughly understood. They are indeed so very different that they are practically mutually exclusive. These two aspects are *visual sensitivity* and *visual acuity*. By the sensitivity of an eye we mean its ability to respond to weak stimuli, the capacity it has for continuing to respond to light as that light is slowly dimmed. By acuity we mean the ability to continue to see separately and unblurred the details of the visual object as those details are made smaller and closer together. Sensitivity involves what the psychologist and physiologist call 'threshold of stimulation'; acuity involves what the physicist and optician call 'resolving power'.

Both the sensitivity and the acuity of the vision of any vertebrate depend upon the structure and mode of operation of its entire visual apparatus, including the gross plan of the eyeball, the characteristics of the dioptric media, the retina, the cerebral structures involved in vision, and the mental capacity of the animal. But the structure of the retina sets ultimate, maximal limits upon both sensitivity and acuity which cannot be exceeded by any sort of manipulation of other parts of the whole system. We can therefore understand these two aspects of vision well enough for the time being, if we examine the retinal basis for each.

Retinal Factors in Acuity—To consider acuity first: if the reader will carefully compare a newspaper picture with one printed on the glazed paper of a magazine, he will see that each is composed of dots, and that the two pictures differ greatly in amount of detail. The news-

paper picture is built up of large dots spaced widely, for on such rough paper any finer dots would make only an inky blur. The magazine photograph contains many more dots per unit area, and they are much smaller. We say that the magazine picture is the better resolved of the two. Similarly, we might take two photographs with the same camera but using two different kinds of film whose emulsions differed greatly in fineness of grain. The fine-grained picture could be enlarged much more than the coarse-grained one without becoming blurry and losing in detail. The fine-grained emulsion 'resolves' better what it 'sees'. Again, through a well-corrected microscope lens one can see and count fine dots, striations and the like which run together under less perfect lenses—and again, we speak of a difference in resolving power as existing between the two. As we have seen, retinal images are very small; but mental images are 'big as life' and the retinal image must stand enormous enlargement without too much loss of detail, when it is translated into a mental picture of the visual field of the eye.

The dioptric apparatus of the eye may cast upon the retina an image which is relatively large or small, hazy or sharp; but the retina in turn may be crudely or finely built and upon this will depend the possible maximum perfection of the cerebral image. The resolving power of the retina is governed by three factors, all of which vary from retina to retina and the last of which may even vary physiologically from time to time within a single retina: (*a*) the slenderness of the visual cells; (*b*) their closeness of spacing; and (*c*) the number connected with one optic nerve fiber. The first two of these are almost self-evident; for if the images of two object-points fall upon two separate visual cells, between which is an unstimulated visual cell, the two object-points may be resolved; but if the visual cells are so plump or so far apart that the two object-points are imaged upon two *adjacent* visual cells, they cannot be distinguished as two points and will seem the same as a single large object-point whose image covers the same two adjacent visual cells. In the one case, we have an analogy for the fine screen through which a picture is photographed for reproduction on coated paper as a half-tone electrotype; in the other case, a coarse screen like that used with newsprint.

Factor "*c*" brings in the concept of summation presented in a preceding Section. Two object-points, whatever their size or separation, will be seen as a single blur if their images fall upon visual cells which connect with the same bipolar, or upon those whose separate bipolars

connect with the same ganglion cell. Other things being equal, the more bipolar and ganglion cells in a retina, the higher its resolving power. Two retinæ may be about equal in this regard even when one has many slender, tightly packed visual cells and the other has fewer, plumper, more widely spaced ones; for in the first retina there might be many bipolars but few ganglion cells, or fewer bipolars and more ganglion cells, and the overall resolving power be no greater than that of the second retina whose visual cells were scanty and large—provided they had isolated bipolar and ganglion-cell connections.

When sections of the retina are especially prepared so that its nerve fibers and their connections are brought out, the retinal foundation for the visual-acuity tenet of the Duplicity Theory is at once evident. Rods are always connected in large numbers to single bipolar cells while cones tend to have more isolated connections (Fig. 19, p. 43). Of the many forms of bipolars in the human retina, the smallest (midget bipolars of Polyak) each tend to be connected with a single cone and in turn to an individual ganglion cell and optic nerve fiber, so that each such cone has a 'private wire' to the brain; whereas, to extend the telephone analogy, other cones and especially rods are on the old-fashioned multiple 'party line'.

This great difference in the degree of summation of rods and cones is the most important single factor in making rod vision diffuse and cone vision sharp. It is much more than enough to compensate for the fact that in almost all retinæ the rods are more slender than the cones, which would give the rod-population the *higher* resolving power if the degrees of rod- and cone-summation were made equal. Thus the chief reason for the crude character of rod vision is outside of the rod itself; and we should so state the Duplicity Theory that it attributes acuity differences not to the rods and cones themselves but to the entire rod-vision and cone-vision mechanisms, each including a set of visual cells and their particular bipolars, ganglion cells, and optic nerve fibers. Relatively few bipolars connect with both rods and cones and probably a minority of ganglion cells embrace both rod- and cone-bipolars. Parinaud's 'théorie des deux rétines' is thus really more expressive of the facts than is 'Duplicity Theory'. The most recent and accurate estimates of the number of rods and cones in one human retina are: rods, 110,000,000 to 125,000,000; cones, 6,300,000 to 6,800,000 (Østerberg). There are about 1,000,000 fibers in the human optic nerve, not all of which are sensory; and in a sizable group of these (the macular bundle)

each fiber represents a single, unsummated cone. Obviously, summation is very great even in the human retina—and the human eye is built, better than most, for 'sharp' vision!

Another important cause of the haziness of rod vision is the dilatation of the pupil. To have only the rods in action, the illumination must be dim—below the threshold of stimulation of the relatively insensitive cones. The pupil opens to let in more light, which permits the rods to continue in action but, incidentally, has two unfortunate effects: the 'depth of focus' of the eye is reduced, and the periphery of the lens comes into play with its detrimental effect upon the quality of the optical image. There is nothing the retina can do about it, and twilight vision here suffers another loss in resolution for which the individual rods should not be blamed. In animals whose eyes are built for moonlight, this factor may be negligible or absent since the lens is then large, and the whole area of its surface exposed by the widened pupil is probably optically 'good'; but the retinal summation factor is still present in such animals, and indeed in far greater degree than in ourselves.

Retinal Factors in Sensitivity—The differences between rod- and cone-vision with regard to sensitivity are, like the acuity-differences, caused by three factors. They are not unrelated to the acuity-differences, and in the case of sensitivity two of the factors reside in the visual cells themselves and only one is extrinsic. The sensitivity-promoting factors in the rod mechanism are: (*a*) the size of the outer segment; (*b*) the extent of summation; and (*c*) rhodopsin.

The business end of a rod or cone is its outer segment. It is in this part of the cell, nearest the pigment epithelium and thus farthest from the source of light, that the light effects chemical changes which initiate the impulse that travels down the length of the cell and, if it is strong enough, evokes a nerve-impulse in the associated bipolar. By and large, rod outer segments tend to be long cylinders whereas cone outer segments are shorter (Figs. 22-26); and while these may be as thick through at their bases as rod outer segments, they taper more or less and may even be quite pointed at their tips. Hence the names originally applied to the two types of cells, though the human cone outer segment is now known not to be at all conical when properly preserved.

If a geometrical cone and a cylinder have the same area of base and the same height, the cone then has only one-third of the volume of the cylinder. Here is an important intrinsic reason why, other things being

equal, a rod should be more sensitive to light than a cone—several times as much photosensitive material is traversed by a pencil of light, when it stimulates a rod, as when it stimulates a cone. Thus in dim light sufficient chemical change may take place in a rod for an effective impulse to reach the bipolar; but the same amount of light will not lead to activity in a cone-bipolar alongside. The rod, then, will have the lower threshold of stimulation—it will take less light to set off its transmission of an impulse. Rods can lower their thresholds in evolution (thus increasing their sensitivity) by lengthening their outer segments as long as this does not interfere with the nutrition of the rest of the retina from the choriocapillaris. Cones could of course also increase their sensitivity by elongating and by approaching a cylindrical form; but they have not often done so, except as a part of the process of transmuting into rods.

The second factor influencing sensitivity is the extent of summation. If several visual cells are hammering at the door of a single bipolar, it is more likely to be aroused than if a single visual cell has to try to evoke a bipolar response without aid from others. Nerve cells carry impulses in obedience to the 'all-or-none law', which means that if a given fiber conducts an impulse at all, it transmits it at full strength. The visual cells, however, are not nerve cells (see Chapter 5, section B) and there is no evidence that their foot-pieces obey the all-or-none law. We are consequently free to suppose that when even a little light strikes a rod, something happens photochemically, and that several feeble impulses travelling down several rod foot-pieces and impinging upon one bipolar dendrite can start an impulse flowing in that bipolar. In the same weak illumination, a single cone or even a rod would not carry an impulse strong enough to awaken a private bipolar.

Indeed, unless the function of the multiple connections of rods to bipolars is to promote the sensitivity of the whole rod-mechanism in this way, the inward convergence of the retina becomes quite meaningless. Summation tends to destroy visual acuity, and no animal needs or wants diffuse vision for its own sake—he only tolerates it if he must do so in order to gain the sensitivity which happens to be more important to him.

Bulky visual cells and extensive summation promote sensitivity, but it is inevitably at the expense of visual acuity. *Sensitivity and resolving power are thus on the two ends of a see-saw, and whatever sends one up, sends the other down.* This relationship holds as well for extra-retinal structures as for the retina itself; for the big lenses and wide pupils of some vertebrates, which produce small bright images and lower the

overall ocular threshold, reduce acuity; and in others the flat lens which produces a broad image, spreading over enormous numbers of visual cells, thereby increases the resolution but at the same time lowers the brightness of the image and thus reduces the sensitivity of the eye as a whole.

By far the most important factor in endowing the rods with their great sensitivity is the substance which is called 'visual purple' or better, rhodopsin. This is a deep red pigment which is formed slowly but continuously in the rod outer segment. The greater its concentration there, the more light is absorbed and the more effective is that light as a stimulus for vision. Since rhodopsin is destroyed by light, it builds up to higher concentration in dim light or darkness than in bright light. Thus

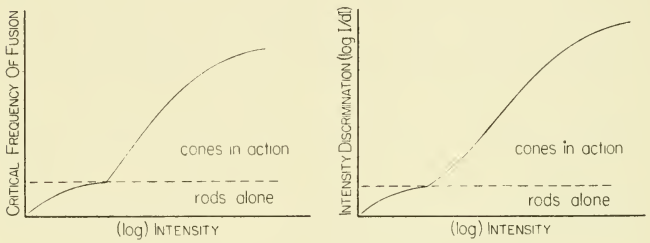

Fig. 27—Evidence for the Duplicity Theory (see text).

the sensitivity of the rods automatically increases just when it will do the most good, due to the excess of rhodopsin-formation over destruction, and decreases when that in turn is desirable, due to the excess of rhodopsin-destruction over formation, in bright light. Moreover, the employment of rhodopsin for increasing sensitivity does not entail any sacrifice of resolving power by the rod-mechanism, and there are few vertebrates whose rods get along without it.

It is rhodopsin which is largely, perhaps entirely responsible for 'dark adaptation', the familiar result of which is our ability to see quite well around us in a theater after a few minutes in our seat, although we may have had to feel to see whether the seat was empty, when we first came in.

Rhodopsin is entirely absent from cones at all times; and there is perhaps so little of it in rods when they are brightly illuminated that they must then fall back upon the intrinsic outer-segment-volume factor and

the extrinsic summation-difference to retain any lead over the cones in the matter of sensitivity. But when the rods are working to best advantage, at intensities below the cone threshold, the intrinsic factor of their rhodopsin content far outweighs the combined effect of the other two. So important is rhodopsin in this regard, and so deeply involved in the fundamental chemical events of the visual process itself, that a large part of the first section of the next chapter will be devoted to this magic chemical whose effect is: "Now you don't see anything; *now* you do!"

Evidence for Duplicity of Vision—Essentially, then, the Duplicity Theory states that the retina contains a sensitivity mechanism and an acuity mechanism, and identifies these with the rods and cones respectively. If both of these mechanisms are in operation only through a

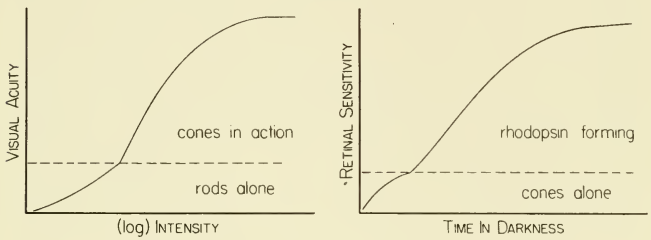

Fig. 28—Further evidence for the Duplicity Theory (see text).

certain transitional range of intensities, and only one or the other of them can operate effectively below and above this range, we might expect that many phases of visual physiology would exhibit differences in accordance with whether one, both, or the other mechanism were in action. This is indeed the case. When graphs of various visual physiological processes are plotted, a characteristic 'kink' is always to be seen in the curve, marking the change-over from predominantly rod- to predominantly cone-control of the process in question. Moreover, when such curves are plotted for stimuli restricted to the pure-cone (foveal) portion of the human retina, or are plotted for animals with cone-simplex retinæ, there is no kink—the whole curve resembles the cone portion of the graph of a rod-and-cone, duplex, retina. And of course pure-rod retinæ yield curves which lack kinks and simulate the below-the-kink portion, or rod portion, of a duplex retina's graph.

The kink is often sharper than we might expect it to be, if it represents a transition. It is accentuated—that is, the overlap of rod-functioning into the physiological realm of the cones is reduced—by little-understood phenomena of mutual inhibition of rods and cones. Circumstances which favor one of the mechanisms allow it somehow to suppress, partially, the activity of the other mechanism. Thus the rods or cones of a 'pure' retina in some ways exceed in performance their counterparts in a duplex retina.

When the rate of flashing of an intermittent light is speeded up, a point is reached at which the successive impressions fuse and the light appears to burn steadily. This 'critical frequency of fusion for flicker' has been much studied in man and animals—in the latter by indirect methods, of course, involving training or the recording of the electrical discharges from the retina. The critical frequency increases with intensity (strictly, with the logarithm of intensity— = Ferry-Porter law). At an intensity of 0.25lux—the cone threshold—the critical-frequency curve of a duplex retina such as the human shows a kink (Fig. 27). When colored lights are used, the effect of color on the critical frequency begins to manifest itself only above the cone threshold, as would be expected. With red light, there is no kink—the rods being insensitive to deep red, however intense. Only the cone part of the flicker-fusion curve is obtained from foveal stimulation; and, the farther peripherally the area stimulated, the closer the whole curve simulates that part due to the rods alone. A pure-cone retina, such as that of a turtle, gives a kinkless curve. The pure-rod gecko has also been found to give a homogeneous curve—though the curve is that characteristic of *cones,* which seems surprising until one takes into account the fact that the geckoes' rods were secondarily derived from cones (see Fig. 25).

Another visual phenomenon which plots a kinked curve is the threshold of intensity discrimination. By this is meant the proportion by which a light must be increased in intensity in order for it to be seen to have brightened. The initial intensity being designated "I", the increment is "dI". The curve of "I/dI" plotted against "I" (Fig. 27) shows a change of slope, or kink, at the cone-threshold intensity. With only foveal stimulation there is again no kink; nor is the rod part of the curve, or any kink, obtained with red light.

Perfectly familiar to all is the increase of visual acuity with intensity —so very commonly do we speak of a light as being "not bright enough to read by." Less apparent is the existence of a kink in this relationship

as well, with acuity rising more rapidly above the cone threshold than below it in most animals (Fig. 28). If we knew very accurately this relationship for pure-rod and pure-cone animals, we would expect to find their curves of acuity-versus-intensity to be kinkless.

As a final illustration of the difference in behavior of rods and cones, we shall consider the rate of dark adaptation, or increase in sensitivity in darkness following exposure to bright light. The graph of this increase (Fig. 28) again shows a fairly well-defined kink owing to the fact that the cones reach their maximum sensitivity at a rapid rate before the sensitivity of the rods begins, slowly, to increase at all. In pure-rod, duplex, and pure-cone eyes the expected differences in the slope of the curve, and in the presence or absence of a kink, are indeed found when such criteria of sensitivity as the behavior of the pupil or the electrical discharges from the retina are recorded.

We have surely seen enough evidence now to convince ourselves of the duplicity of the visual process. The complexities of the above evidence may seem rather appalling to the innocent reader; so, let us try, in the next chapter, to make the process of vision seem fairly simple after all!

Chapter 4

THE VISUAL PROCESS

(A) Scotopic Vision

Any attempt to depict the events which intervene between the impact of light upon the retina and the registration, in consciousness, of the qualitative and quantitative aspects of vision, must necessarily be largely guess-work, and can be lucid and connected only if it is dogmatic. The following treatment is such an attempt, made for the sake of the reader rather than for the sake of the subject. The literature of the field of visual physiology is vast and unorganized, and largely unreadable without a considerable background of mathematics. Paraphrased *sans* mathematics, it is bound to seem largely a series of unfounded generalizations to any astute physiologist who may read it; but, these latter gentry have yet to promulgate an inclusive theory of vision in which a sophomore cannot pick great holes. In the present state of knowledge, one description of what goes on in vision is almost as good as another, and may be the best one for the beginning reader if, at least, he is able to follow it without miring down in equations.

Rhodopsin—Perhaps the greatest advance which has ever been made in this field was the discovery of the photosensitivity of the rod pigment, rhodopsin, by Boll in 1876, and the elucidation of most of its properties by Kühne in the years immediately following. But rhodopsin was at first used to explain too much, and during its history many of its original attributes have had to be taken away from it. Physiologists have relinquished their beliefs about rhodopsin most reluctantly, since the less one can credit to it, the farther away seem the solutions of some of the fundamental problems of vision. However, in very recent years some progress has been made in the study of other photosensitive substances in the retina, which may be found to do some of the things formerly credited to rhodopsin itself.

Rhodopsin was once supposed to be the *sine qua non* of all of vertebrate photoreception, and owing to the attention it commanded, photochemical theories of vision rapidly came to be the only ones seriously considered. But it was soon seen that if vision does have a strictly photo-

chemical basis, no one photosensitive substance could be entirely responsible for color vision—at least three such substances are required by the long-popular Young-Helmholtz theory, and even more were demanded by some other theories of color vision. Rhodopsin might be one of these—but where were the others? The resuscitation of Schultze's ideas in the form of the Duplicity Theory made it necessary to abandon rhodopsin as a color-vision photochemical, for it was finally made certain that some vertebrates have none of it, and that it never occurs in cones. Still, there were those who believed that vision as such—brightness-vision both photopically and scotopically, apart from hue perception—necessitated rhodopsin. These workers argued that there must be invisible traces of the substance in cones in order to account for their light-sense; and this idea has been very long a-dying.

Rhodopsin is still widely regarded as the absolutely essential photochemical substance for rod activity. Even this is an unnecessary belief, since rhodopsin may be nothing more than a sensitizer, so powerful that its action masks that of another, essential, material so completely that the brightnesses of lights are directly related to their effects upon rhodopsin.

The substance is a reddish pigment whose chemical nature is not yet completely known. It is released from the rod outer segment by substances which lower surface tension, such as bile salts, saponin, digitonin, sodium oleate and salicylate, and snake venom. It forms a precipitate with platinic chloride—an insoluble yellow compound which can be seen in the rods in permanent microscopic preparations made of retinæ which are kept in darkness for an hour or so before preservation.

Rhodopsin is commonly described nowadays as a hydrocarbon conjugated with a protein, through a belief that vitamin A—essentially a hydrocarbon—is an important constituent (*v. i.*). The molecular weight of rhodopsin is about 270,000. This and other features make it clear that most of the molecule is proteinous; but of course to say that rhodopsin is essentially a protein is like saying that dynamite is essentially fuller's earth. The business part of the molecule—its 'chromophoric' (color-bearing) group—is neither a hydrocarbon nor a protein, though it may be derived indirectly from a portion of the vitamin A molecule. The latest information* is that the rhodopsin molecule contains a protein, 'provisual red', and probably a third substance. The chromophore, provisual red, can be split into a fatty acid and 'visual red'; the latter in

*Kindly supplied by Dr. Arlington C. Krause in advance of his own publication thereof.

turn can be made to yield 'visual yellow' and 'indicator yellow'. Certain of these photosensitive substances have previously been identified as partial-breakdown products of rhodopsin when it is struck by light.

The most important properties of rhodopsin are its intense coloredness, its sensitivity to all visible wavelengths excepting those deep red ones which (by reflection from it) give it its own color, and the fact that its response to these wavelengths is to disrupt into colorless or pallid substances of little or no photosensitivity. It is most affected by the blue-green region of the spectrum, centering at about $\lambda 500 m\mu$. One might expect that this wavelength would appear brightest to the dark-adapted eye in which rhodopsin has built up to a high concentration. Owing however to modifying factors (chief of which is believed to be the high absorption of short-wave light in the ocular media), the brightest point in the scotopic spectrum is shifted red-ward, to $\lambda 510 m\mu$. One of the two or more substances into which rhodopsin is broken down by light is presumed to irritate the protoplasm of the rod and cause a wave of electrochemical activity, much like the impulses which flow along nerve fibers, to pass down the rod foot-piece and stimulate the bipolar neuron.

Dark Adaptation—Rhodopsin is not as all-important as it was once thought to be, but it is largely responsible for the ability of the rod to 'dark-adapt' or lower its threshold—until the amount of light needed to stimulate it is a tiny part of that required to arouse a cone. While we are in ordinary daylight there is believed to be but little rhodopsin in our rods, for the concurrent processes of its synthesis and breakdown are then in equilibrium at a sub-maximal concentration of the substance. When we enter a dark place the process of adaptation to dim light begins at once, since the breakdown all but ceases while the upbuilding of new rhodopsin continues at the usual rate. In the dim light, a new balance is struck at a high concentration of rhodopsin, so that a given amount of additional light will now appear brighter than before, since it destroys a greater absolute amount of the photosensitive pigment.

Rhodopsin is not quite the whole story in dark-adaptation, however. The dilation of the pupil, upon going into a dim or dark place, admits more light to the retina, so that the overall sensitivity of the eye increases somewhat, apart from any change in the retina itself. In the latter, the first step in dark adaptation is taken by the cones rather than the rods, for the tiny amount of photosensitive material which they ever contain is very quickly built up to a maximum (see right half of Fig. 28).

Then, too, a part of dark-adaptation—it is hard to say how much—is accomplished by switchboard effects in the integrative layers of the retina, bringing about temporary hook-ups, to ganglion cells, of larger numbers of visual cells than usual.

In dim light or darkness, the destruction of rhodopsin having largely or wholly ceased, the new formation of the substance (partly from the decomposition products still present in the rods, partly from new raw material absorbed from the pigment epithelium) quickly restores the concentration to a fairly high level. Within seven or eight minutes, in fact, the previously depleted rod becomes capable of function. The rods are now deeply colored and absorb much more of whatever light may strike them, so that a strong impulse impinges upon the bipolar. Should we now emerge into a bright place, the light would dazzle us uncomfortably until enough rhodopsin had been destroyed to raise the thresholds of the rods considerably. This process takes a much larger fraction of a second than is required for the pupil to constrict. So, the removal of some of the rhodopsin is the controlling factor in *light*-adaptation—which we might loosely define as the destruction of excessive sensitivity. The pupil slowly reopens as the sensitivity of the retina is decreased, and attains a final 'physiological size' appropriate to the particular species of animal, and which for man is maintained in all intensities between 100 and 1000lux—the range within which, presumably, an equilibrium can be maintained in the photochemical system of the visual cells.

Rhodopsin accumulates to a considerable proportion of its maximum in half an hour and is almost at maximum in an hour; but it continues to form slowly for twenty-four hours or more. If anything essential for its manufacture is deficient in the individual or in his diet, the rate of formation will be greatly retarded, and the greatest amount ever formed will be much less than normal. This condition of deficiency leads to nyctalopia or night-blindness, in which dark-adaptation is incomplete and the individual feels the handicap when trying to make his way about in dim places and at night. He may become a menace to his fellows if he drives an automobile at night and meets many bright headlights which assault the little rhodopsin he is able to form. In the armies of years ago, night-blindness—common under conditions of malnutrition—automatically exempted a soldier from nocturnal guard duty. In modern warfare, the night-blind individual is particularly useless in defense against nocturnal bombing, and every effort is made to maintain a high concentration of rhodopsin in the retinæ of night fighter aircraftsmen.

The substance whose lack is the usual cause of nyctalopia was shown in 1925 to be vitamin A, a colorless material manufactured in the liver from carotene, a reddish plant pigment. Although there are types of nyctalopia which are hereditary, and the condition also occurs as a symptom of degenerative retinal diseases, in its various degrees it is usually the first detectible sign of vitamin A deficiency. Nutritionists and pediatricians are consequently much interested in attempts to devise clinical tests—by which they mean quick and easy ones—for nyctalopia; but for various reasons a reliable test which is really simple seems hardly possible, and the literature of the subject reveals more and more pessimistic statements.

Soon after 1925, the obvious conclusion was drawn that vitamin A is the precursor of rhodopsin, that it is actually converted into that substance, and may be formed again when rhodopsin is disrupted by light. Elaborate diagrams of this closed circuit, with the supposed intermediate compounds, are commonly seen in print. But the most recent and careful chemical studies of rhodopsin itself (*v. s.*) have greatly weakened our faith in a direct genetic relationship between it and vitamin A. All that can be safely said at the moment is that the vitamin is essential for the synthesis of rhodopsin, probably as a minor contributor rather than as a principal raw material.

Rhodopsin may be the essential, the one and only photochemical substance that is ever present in rods, but there is no proof that this is so. There are rods which contain none, though perhaps in all of these (*e.g.,* in *Sphenodon, Xantusia, Phyllorhynchus*) the lack of rhodopsin is owing to these rods' having had relatively recent origin from cones. They presumably get along perfectly well with the photochemical system inherited from their cone ancestors—for all anyone knows at present, the complete color-vision mechanism may still be functioning in them. The photochemical substance or substances in cones may indeed have chemical kinship with rhodopsin, for it has recently been reported that the dark-adaptibility of the cones (which in terms of intensity-limit *ratios* is actually about equal to that of the rods) is influenced by the dietary intake of vitamin A.

Just a few years ago, it was being claimed by the Finnish retinal physiologists associated with Ragnar Granit that when a rat retina has been so brightly illuminated that all of the rhodopsin is bleached, the optic nerve no longer carries the electrical discharges which can normally be detected in it during photic stimulation of the retina. This was hailed

as proving conclusively the complete dependence of rod vision upon rhodopsin. But workers in the same laboratory have more lately obtained puzzling indications that very little rhodopsin is ever normally bleached in the intact animal. They found apparently normal amounts of it in eyes whose electrical responses had been reduced one-third to one-half by stimulation with light. Possibly the electrical responses would entirely disappear while there was still a great deal of rhodopsin in the rods. This might be new evidence that rhodopsin is a secondary sensitizer rather than a primary photosensitive material, or it might only mean that switchboard effects in the retina are more important in light-adaptation than we have been supposing.

Whatever its whole meaning may be, rhodopsin was a clever invention; for its light-absorbing power makes it responsive to weak light, yet it conveniently bleaches when, in bright light, the full amount of it would greatly handicap the animal. Even the particular color it possesses is in itself adaptive, as will be elucidated later (Chapter 12, section A). So elaborate a substance could hardly have been present in the 'original' provertebrate visual cell, which must then have been high-threshold, more like the cones we know than like a modern rod. Some of the photosensitive ancestor-cells of the rods and cones were left behind in the brain lining when the eyes evolved, as will be brought out in the next chapter. These, though sensitive enough to respond to light through the entire wall of a bird's head (as shown by their reflex control of spermatogenic activity), contain no rhodopsin as far as we know. If the modern rod cell depends utterly upon rhodopsin for its photosensitivity as such, it has come to do so secondarily by discarding some more ancient photochemical for want of efficiency under scotopic conditions.

Rod Vision—We may conceive of the peripheral (ocular) portion of the rod visual process as taking place somewhat as follows: At the start of adaptation to dim light there is little rhodopsin in the rods, and so little of this is broken down by the weak light that only feeble impulses pass down the foot-pieces. As the amount of rhodopsin increases, a greater absolute amount is broken down by a given light and the impulses become stronger. Those bipolars with which the largest numbers of rods connect now receive enough total stimulation to be set off into conductive activity, and they begin to carry nerve impulses at a certain low frequency of discharge—each bipolar acting somewhat like a reservoir and, so to say, filling up with stimulation and discharging an im-

pulse, the frequency of discharge thus bearing a relation to the amount of stimulation.

The attached ganglion cells now behave similarly and conduct in synchrony with the activity in the bipolars. The electrical aspect of their discharges can be picked up in the optic nerve as action currents with proper amplifying and recording devices. In the brain, a sensation of light is now aroused whose strength depends upon the resultant of the number of active nerve fibers and their frequency of discharge. As dark-adaptation proceeds further, the number of rods per unit area of the retina whose activity actually registers in consciousness steadily increases, due to the activation of more and more bipolars having smaller and smaller numbers of associated rods. As the mosaic of functional receptor units becomes more and more dense, visual acuity rises hand in hand with the rise in the strength of the brightness sensation. When dark-adaptation is complete, both visual acuity and brightness are maximal for the intensity being supplied, and any further increase in either will depend upon an increase of illumination above the threshold of the cones, thus bringing the latter into play. The destruction of rhodopsin may then increase to such an extent that the brightness would decrease in the face of increasing objective intensity—in other words, light adaptation would have commenced. Incidentally, rising intensities above the cone thresholds naturally bring into action more and more cone bipolars and associated ganglion cells, so that visual acuity continues to rise until all elements are functioning. Beyond this point, further increase of intensity brings no additional visual acuity—though of course *brightness* can increase until all involved optic nerve fibers are discharging into the central nervous system at their maximum rates.

If, with the retina thoroughly dark-adapted, it is now subjected to bright light, rhodopsin is immediately broken down in large amounts in all of the rods which are receiving stimulation, and all of their associated nerve fibers begin to conduct at high frequency. As the rhodopsin fades, however, the rod thresholds rise and the frequency falls off. As the rod thresholds approach those of the cones, a comfortable brightness is attained with the pupil now reopened, and with the rods perhaps still all in action, contributing all that they ever can to the resolving power of the retina—considering that they are of course still summated. In comfortable illuminations above the cone threshold, however, the cones are contributing only a part of their potential resolving power, which becomes maximal only at intensities above 100lux.

(B) Photopic Vision

Cone Vision—Turning now to the cones, we are confronted with the complex matter of color vision—assuming for the nonce that all cone-bearing vertebrates do discriminate hues. We can imagine subtracting color vision from the whole performance of the cone—but what we would have left, we could describe in terms of a rod mechanism that had little summation and very little rhodopsin. So, we cannot well avoid considering the elementary and purely qualitative aspects of color vision if we are to attempt to picture the mechanism involved and thus round out our survey of visual physiology.

Color—Color, or better, 'hue', exists only in the mind. No light or object in nature has hue—rather, the quality of hue aroused as a sensation is projected back to the object as one of its attributes, just as the patterns of brightness and darkness in consciousness are projected back into the visual field to endow objects with their size, shape, tone values, and movement. For, we perceive *objects* rather than lights. We can see objects falsely as to size, shape, and motion, and just as falsely as to color since color is purely subjective. The color of a surface depends not only upon its chemico-physical nature, but also upon the kind of light by which we see it, and upon our memory of the impression it may have given us under some more familiar illumination. Thus, a particular dress may look red only in daylight, yet we still call it red under an artificial light when it may actually be reflecting more yellow light and should then be seen as orange.

The hue sensation aroused by a light depends primarily upon the frequency of its vibration, usually expressed as the distance between successive waves in the vibration, the wavelength. The longest visible wavelengths, in the neighborhood of 760mμ, arouse the sensation we call red; the shortest ones, around 390mμ, give us the sensation of violet, which must be seen in a spectroscope to be appreciated (since the violets of textiles and pigments in general are not true violets, but diluted purples). In-between wavelengths give us the other hues of the spectrum.

When all of the visible wavelengths are being received on the same area of the retina, either simultaneously or in such rapid succession that their physiological images persist long enough to overlap or fuse, we see what we call white light. The removal of some wavelengths from the full assortment makes the remainder of the light appear, collectively, as a color. Such a removal may be effected by selective reflection or by selec-

tive transmission. An opaque colored paper or cloth performs the former, a translucent colored glass or liquid performs both. A colored object *is* colored, instead of gray, because it absorbs some wavelengths and reflects or transmits others. The latter being the ones which reach the eye, they determine the color of the object. If the object is specially illuminated only by wavelengths which it can absorb, it can reflect none of them and will then appear black. An object which in sunlight appears black must,

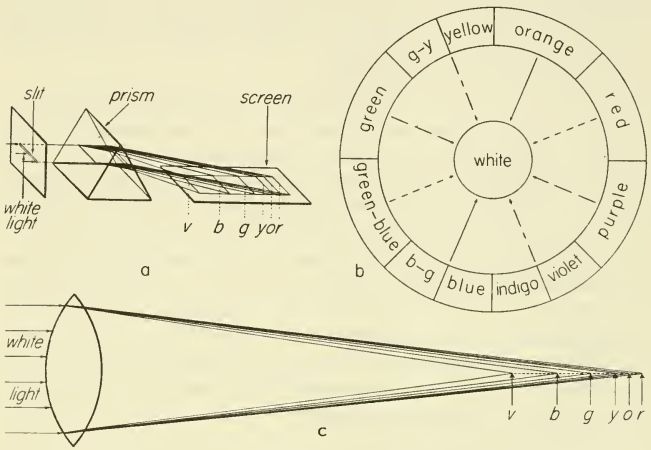

Fig. 29—The physical and psychological spectra.

a, the visible spectrum as formed by a prism.
v- violet; *b*- blue; *g*- green; *y*- yellow; *o*- orange; *r*- red.

b, the psychological color circle. Red and violet intergrade through purple; diametrically opposite hues are complementaries, and make white when mixed in correct amounts.

c, the linear spectrum formed by a lens. The distance from the focus of violet to that of red (greatly exaggerated in the diagram) is the 'linear chromatic aberration' of the lens.

then, be one which absorbs all wavelengths, just as white objects, to appear white, must reflect all. Of course no object absorbs or reflects all of the light striking it. Whether it reflects all wavelengths equally, or some more than others, it reflects only a certain percentage of the light energy. This percentage is the object's reflection coefficient or 'albedo'.

No object can reflect only a single wavelength, and hence no object can have a pure color. To obtain pure colors, we must select them from a

band spectrum by means of a slotted diaphragm. Such a spectrum is formed automatically when a mixture of wavelengths, such as sunlight, is passed through a narrow slit and then through a prism. Since the refractive index of the glass is different for each wavelength, being highest for violet and lowest for red, the colors are sorted out of the mixture and can be caught on a screen, all in order, as a spectrum (Fig. 29a). If the light reflected or transmitted by a colored object is concentrated and passed through a prism, the spectrum formed will naturally have lightless regions in it corresponding to the wavelengths whose removal from the sunlight, through absorption by the object, gave the latter its color. Such a spectrum is an 'absorption spectrum', and is the basis of spectral analysis, that powerful weapon of chemistry and astronomy with which substances are detected by means of their specific fingerprints on sunlight.

With a little practise, a normal person can learn to distinguish about one hundred and sixty distinct hues in the sunlight spectrum.* If we now let any two of these hues escape through narrow slits and aim them with mirrors at the same piece of paper or ground glass, or look at one with each eye, or present them in rapid alternation to one or both eyes, we will obtain a sensation different from that given by either hue alone. In most cases, the sensation will be that afforded by some other pure hue, lying between the chosen two in the spectrum. If however the latter are far apart in the spectrum, and lie diametrically opposite each other on the 'color circle' (Fig. 29b), they are 'complementaries' and their mixture will produce *white* light. Thus any hue in the spectrum (and white) can be produced by mixtures, made by one means or other, of some two other hues. Some white light may need to be added to the spectral hue in order to make it an exact match for the mixture. We are not of course discussing here the subtractive mixtures which one obtains by stirring pigments together—the artist's complementary, primary, and secondary colors have nothing to do directly with those of the physiologist.

The physiologist often terms red, green, and violet 'primary' colors, because in none of them can any other hues be seen. Yellow is also considered a primary by psychologists, as is blue for that matter. Yellow sensations can be produced by means of simple apparatus which presents red to one eye and green to the other, but yellow is not reddish green or greenish red. Yellow, in this instance, is obviously synthesized in the

*Actually, 160 complexes of hue-plus-whiteness. No one has ever yet determined the (much smaller) number of hues which would still be discriminable, were saturation eliminated as a variable.

brain—probably also, as we shall see, even when it is excited monocularly by monochromatic yellow spectral light. We can, if we like, make an artificial distinction among the psychological primaries, between those which can be easily produced by mixtures and those which cannot; but even red and violet, though at the ends of the spectrum, can be produced by mixtures. The spectrum really has no ends—it only seems to have, due to the way in which a prism forms it. Really, it is a closed entity, for red and violet are *adjacent,* psychologically—their mixture results in purple, which lies outside the spectrum but fills the gap between red and violet in a spectrum which we might imagine bent into a ring (Fig. 29b).

Though the primaries can all be synthesized, they cannot be analyzed —which is what makes them primaries. In orange one can discern both the red and yellow components; in purple, the blue and red. But though blue can be made by mixing green and violet, it does not look as though it contained either. Yellow and violet, and red and green, are sometimes called 'disappearing color pairs', since when the members of such a pair are mixed, neither member can be seen in the mixture.

The mixture of three properly chosen primaries (the most convenient are red, green, and violet—and these three *do* have, in a certain way, an edge on the other two chief primaries, yellow and blue) arouses the colorless sensation of white or gray, which is also afforded by mixed complementary pairs of colors such as orange and green-blue, green-yellow and violet, red and blue-green, etc. In each such pair it can always be noted that at least one member is not a simple color or primary; and the two members, between them, always contain red, green, and violet or can be matched by mixtures of them in pairs. The complement of any hue can also, obviously, consist of white light minus that hue. A mixture may be complemented by a pure hue, and the latter by one other pure hue, by simple or complex mixtures, or by white minus the first pure hue.

Saturation—The whole of the sensation aroused by a colored light or object has aspects other than hue itself. It has brightness of course, the psychological counterpart of physical intensity as with achromatic stimuli; and it has saturation. Saturation means coloredness as apart from color, and *quite* apart from brightness. In a darkroom we could aim, at the same ground-glass, a beam of pure colored light and a beam of white light. The ratio of color to white in the resulting spot of light would be the measure of its saturation. With more white added, the saturation would go down and the brightness would go up; but instead

of simply adding more white light, we could add some white and subtract some colored light, and thus lower the saturation while keeping the total brightness constant. Again, we could reduce the amount of colored light without adding extra white, and thus reduce both saturation and brightness. Thus it can be seen that the saturation of a colored light has nothing to do with the particular hue involved, and is also quite independent of the brightness.

There are two chief ways in which saturation and unsaturation may be manifested. Firstly, saturation can represent the extent to which a spectral color is free from objective adulteration with white light, or the extent to which a pigmentary color is devoid of admixture with white. Unsaturation of a colored light-beam by mixture with a white beam has been mentioned above. A paper- or cloth-color which reflects much light throughout the spectrum in addition to the strong band of wavelengths which gives it its hue, is a 'tint' of that hue—unsaturated by the white it reflects. An artist, mixing Chinese White with an oil color, is unsaturating that color. Likewise, pigmentary colors may be *apparently* unsaturated by mingling them with black, thus yielding 'shades' of their colors. Admixture with black is really, however, not true unsaturation but is more nearly tantamount to simply reducing intensity and therefore brightness—it is like mixing a light-beam with darkness, which would not unsaturate it even if it could be done! Psychologically, admixture with black is not quite equivalent to reducing intensity, for blackness and darkness are not psychologically identical. Brown, for example, is a black-adulterated color which can be seen as brown only when the conditions are right for seeing black. In a darkroom, a brown area which is not surrounded by lighter areas appears simply as weakly orange or reddish, for the blackness element of the brown becomes mere darkness. If blackness is 'induced' in an orange area by surrounding the latter with white in a darkroom, one can obtain the sensation of brown without resort to pigments, for the orange spot in question need not be pigmentary—it can be formed by filtered or spectral light.

It is important, in thinking about saturation, to keep one's attention upon the amount of color, the 'chroma', present—not upon the character of the unsaturating factor present, for this does not matter. It need not even be whiteness which unsaturates, for, if we wish, we may speak of unsaturating a hue with another hue, and thus think of orange as a red unsaturated with yellow; but this is more than a little dangerous since

so many mixed pairs of colors produce sensations which are not analyzable blends of their qualities, but entirely new qualities.

Apart from the kind of unsaturation which may be produced synthetically so to speak, by mixing into a color some whiteness from a separate source entirely outside the color, there is a type of unsaturation which is inherent in the colored light itself, even in a spectral light of whatever purity. It is as though the monochromatic spectral beam contained some white light which we could not remove. This kind of unsaturation is due to the fact that the visual mechanism for the perception of white is set in operation to some extent by any one wavelength—to a greater extent by some than by others. If we look at a solar spectrum, the yellow region (about $\lambda 580 m\mu$) looks brightest to us, and also looks the least richly colored. We can separate this pallidity of yellow from its high brightness, by turning to a spectrum in which each wavelength represents the same amount of energy. In such a spectrum, the yellow-green region (around $\lambda 557 m\mu$) is now the brightest; but the yellow still seems the least *colored* color, the richness of the chromas increasing from it toward both ends of the spectrum.

This kind of unsaturation, or low chroma, is particularly important physiologically and psychologically. It greatly influences the results of color-mixtures, for the saturation of mixtures is always low. If for example we mix red and green to make yellow, the yellow we obtain is of low saturation as compared even with spectral yellow, and to spectral yellow we must add some white light to make a perfect match with the red-green mixture. The more complex a mixture, the lower the saturation, for we are approaching the result of mixing *all* wavelengths—which is, of course, white itself, with the chroma-content at zero.

The degree of saturation of a spectral light can be ascertained by determining how much of it, added to white, will give that white a hint of chroma. By such means, red and particularly violet are revealed as highly-saturated wavelengths, yellow and green as being of low chroma. We therefore say that the 'white valence' of yellow is high, by which we mean that we can add yellow to another color without altering the hue much more than if we had added the same amount of white. Red or blue, added bit by bit to another color, have more prompt effects upon its appearance—they have a low white valence, cannot take the place of very much white in mixtures.

Recalling that unsaturation is usually accomplished by actual objective admixture with white, we can now see that when the degrees of unsatura-

tion of two 'pure' hues are compared, we are really comparing their intrinsic subjective white-sensation-arousing power, their white valences, or their nearness to whiteness. Yellow is not white, but it is more *like* white than red is, because yellow stimuli more effectively stimulate the whole white-seeing mechanism of the cones and their central connections.

Brightness and the Purkinje Phenomenon—Brightness has the same meaning in cone-mediated sensations that it has in achromatic rod sensations, and is just as independent of actual physical intensity. But

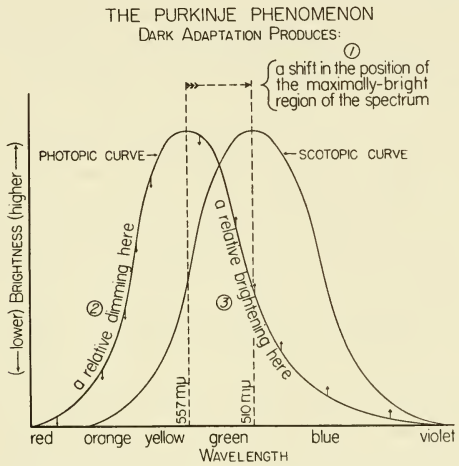

Fig. 30—Graphic depiction of the changes which comprise the Purkinje phenomenon.

the relation of brightness to intensity is different for the cone- and rod-mechanisms. While the brightest part of an equal-energy spectrum is the yellow-green for the cones, it is in the green for the dark-adapted, functionally pure-rod eye. This shift results in a change in the relative brightnesses of colored objects as intensity drops below the cone threshold or rises above it. This change is the 'Purkinje phenomenon', which is simply a betrayal of the change-over from predominantly cone vision to rod vision (Fig. 30; and see Fig. 35, p. 102). It naturally occurs only in duplex retinæ, or duplex retinal areas, and its occurrence is a part of the great mass of evidence for the Duplicity Theory.

It is only by coincidence that the Purkinje shift has the particular extent that it has, in any given retina. The luminosity maxima of the scotopic and photopic spectra might just as well happen to be farther apart in wavelength, or closer together; or even, by chance, identical, for they are determined by very different factors. In the one case, the maximum is determined by the maximum of absorption of rhodopsin—in the other case, by the peak in the resultant absorption spectrum of the photochemical substances in the cones. In some animal with a rhodopsin of slightly different color, and with a slightly different color-vision system, the Purkinje shift might be much greater or much less than in man—or could conceivably be absent (or even might take place in the opposite direction, though no such case is known.)

Trichromatic Vision—The fundamental qualities of cone-mediated sensations, then, are hue, saturation, and brightness. At least a part of the whole process by which these qualities are established in consciousness is essentially physiological. A part of the process is psychological. It would be very nice, considering the avowed scope of this book, if we could carry our treatment of cone vision just to the boundary line and stop. But unfortunately there is no branch of psycho-physiology in which it is more difficult to say where more-or-less 'physiological' *sensation* ends and strictly 'psychological' *perception* begins. Some hues, such as red, green, and violet, appear to be simple sensations. Others, like orange and yellow-green, are mixtures analogous to the sour-sweetness of lemonade or to a chord in music—trained observers can always discriminate the separate elements of the complex. But then there are hues, pure yellow and pure blue, which seem to be more like percepts than sensations, for each is the product of two simultaneously-evoked sensation elements, yet cannot be analyzed into those elements. Here, the sum differs from its parts in a qualitative manner—it is as though when we hybridized horses with zebras, the offspring were always giraffes!

Since the sensations of all hues and white can be aroused by appropriate mixtures of three wavelengths—primaries—chosen from the ends and middle of the spectrum, normal human vision is said to be trichromatic (tri = three). It was an eighteenth-century French printer, LeBlond, who discovered (through a misinterpretation of Newton's writings) that with only seven colored inks, and black, he could print pictures containing the whole gamut of colors theretofore obtainable only with a legion of inks. Being a very economical person, LeBlond experimented further and found that he could get along with only three colored inks. Thomas

Young formulated a theory of color-vision based upon LeBlond's findings, in which he proposed three sets of receptors in the retina, each most sensitive to one of three primary colors. Sensations of non-primary colors were regarded as due to the simultaneous enaction, to varying extents, of two or all three sets of receptors. Whiteness was due to the equal stimulation of all three.

Much support for this three-component theory of color vision was given by Helmholtz in the last century, and nowadays the theory goes under the hyphenated names of the two men. The Young-Helmholtz theory calls for three 'somethings' in color vision; but ideas have changed, from time to time, as to what these somethings are. Young thought of them as three kinds of nerve endings. Helmholtz thought of them as three photochemical substances or processes, which he at first believed to be in three separate sets of cones. Later, he considered that they probably all occurred in each cone.

Other theorists have complicated matters considerably and, in the light of the most recent developments, unnecessarily. The perception of yellow, white, and black formerly gave much trouble and seemed to call for a minimum of four components in cone vision, as in the theory of Hering, the principal rival of that of Young and Helmholtz. The binocular fusibility of red and green into yellow, and the modern concept of the difference between blackness and darkness as being due wholly to contrast, makes the assumption of more than three components unnecessary.

It is entirely likely that the three processes are mediated through each and every cone. White stimuli do not take on hue when made very small in area, as we should expect them to do if they then struck only one or two out of a total of three or more kinds of cones. Again, if there were three kinds of cones with respect to color sensitivity, visual acuity would necessarily be very low in a monochromatic illumination which effectively stimulated only one-third of the cones. But visual acuity is *not* lower in any monochromatic light (except, perhaps, red) than it is in white light of equal objective or subjective intensity; and in some such lights it is even higher. This could mean, as Hecht claims, that all the cone-types respond nearly equally to any given monochromatic light. It can also mean that the cones are all alike—at least in any given small retinal area. They may vary progressively along meridians of the retina, for the number of hues we can discriminate diminishes from the center toward the ora terminalis, unless the intensity is very high. Even this 'deficiency' may really have its basis far from the cones themselves.

Binocular color mixture has been mentioned above, in the instance of the binocular fusion of red and green into yellow. Its existence is fatal to any theory which places the color-vision mechanism entirely in the periphery of the visual apparatus—that is, in the retina. There is no color-sensation, which can be produced by mixing two lights in one eye, that cannot be duplicated by supplying the two lights, independently, one to each eye. If color-mixture *can* be made centrally, one wonders whether *all* color-mixtures, even monocular ones, may not always be synthesized centrally. To suppose so necessitates believing that the optic nerve fibers can simultaneously carry several separate 'primary' kinds of information, which are integrated into a perceptual whole only after reaching some level in the central visual apparatus. To account for binocular color-mixture (and, it can be allowed to account also for monocular mixture) a multiple synthetic mechanism must exist centrally. But it would seem difficult for any one photochemical substance in the cone to be able to give rise to more than one kind of optic nerve impulse. To account for the transmission of simple primary impulses along the optic nerve, when the retina is being illuminated by such a mixture as purple, there must also be a multiple, differentially responsive analytical mechanism in the periphery.

The binocular synthesis of mixed colors and white results in sensations identical with those aroused monocularly by the same stimuli. One reason for this could be that the vision of even one eye by itself is actually carried out through the binocular (fusion) 'center'. This sounds roundabout and improbable, but there is considerable evidence for it. It is difficult to explain otherwise why things look no brighter to us when seen with two eyes than with only one. The functioning of one eye can affect the way things are seen with the other eye. To give only one example: the convergence of a shielded eye causes an apparent lateral movement of a spot of light seen, in a darkroom, only by the other eye —especially when the non-seeing eye happens to be the individual's master or dominant eye. The brain is so accustomed to ascribing most of vision to the dominant eye, that it can be deceived into supposing that eye to be seeing even when it is not, and thus 'sees' the spot of light move in just the way it would have to, to remain visible to the dominant eye during the latter's rotation. The brain is confused as to which eye is seeing what, which could only be possible if the two eyes always formed a team even when only one member of the team works.

The manner in which a mixed color, for instance purple, may be seen by one eye (or both) presented with purple, or with one eye offered red and the other violet, is diagrammed in Figure 31. The purple stimulus in 'a' may of course be steady, or may consist of rapid alternations of red and violet lights; for, as mentioned earlier, fusion of colors may occur temporally as well as spatially. When purple strikes a single retina, impulses somehow tagged 'redness' and 'violetness' pass along the optic nerve to be combined into 'purpleness' by the same central machinery that makes purpleness out of redness from one eye and violetness from the other. In the retina, then, there is some analytical mechanism, two separate parts of which respond independently to the short and long wavelengths in the purple light. We suppose the whole of this analytical mechanism to be a group of (three) photochemical substances.

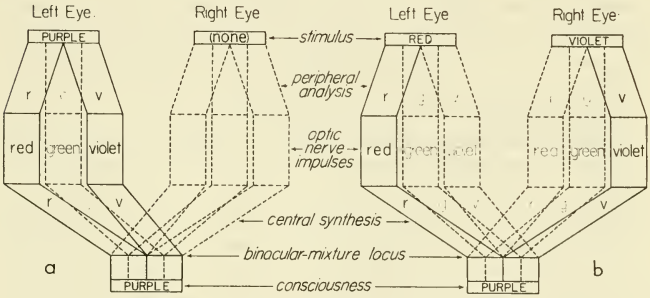

Fig. 31—Perception of a compound color: purple.

a, monocularly (or, a purple stimulus might be supplied to each eye). b, by binocular mixture of red and violet. The inactive components of the visual system are labelled in faint lettering—all components would of course be active in the perception of the all-inclusive compound *white*.

Central Events in Trichromatic Vision—When the dark-adapted eye is presented with an equal-energy spectrum, that spectrum appears colorless (some say, faintly violet) but not homogeneous. At the locus of wavelength 510mμ the spectrum is maximally bright, the luminosity falling off toward the ends and becoming zero, at the long-wave end, at a point corresponding to the orange-red of the photopic spectrum. König and Trendelenburg, around the turn of the century, established

between them the practical identity of this 'scotopic brightness curve' with that of the photopic totally color-blind eye, the absorption spectrum of rhodopsin, and the curve of the rhodopsin-bleaching power of monochromatic lights (Fig. 33, *cf.* Fig. 35). The rods are completely insensitive to deep red because rhodopsin absorbs nothing beyond λ650mμ, and they are most sensitive to green because this kind of light is more avidly absorbed by rhodopsin than any other.

As the intensity of the spectrum is now increased, there is a range of intensity—called the photochromatic interval—within which the spectrum remains colorless. This interval is not the same for all regions. For red, it is of course non-existent, for as soon as wavelengths longer than 650mμ are seen at all they are seen by cones, and are seen *as* red light. In succession toward the violet end, the other hues appear as the thresholds of the cones for them are crossed. The now fully colored spectrum has its brightest part moved (the Purkinje shift) to around λ557mμ, and extends from λ390mμ to λ760mμ. Beyond λ650mμ lies the pure red. At λ600mμ is orange. The exact center of yellow is at λ582mμ, of green at λ515mμ, of blue at λ476mμ. Beyond the indigo of λ424-455mμ lies the true violet (see Table I, p. 4).

In the neighborhood of yellow and blue the change in hue for a given change in wavelength is greatest. To be exact, the two maxima lie at λ580mμ and λ490mμ. Around these values, we can discriminate more different hues, closer together in the spectrum, than we can elsewhere. This is because these wavelengths are maxima in the graph of the intrinsic pallidity or *un*saturation of the spectrum: as we pass from one side of such a maximum through it to the other side, the appearance of the stimulus changes rapidly with a change in wavelength because the ratio of chroma to whiteness in the sensation is changing so rapidly.

The blue maximum, and the minor peak of brightness in this region, may be lowered somewhat by absorption in the yellow pigment of the macula lutea of the retina (see Chapter 8, section D). As the intensity is raised however, yellow and blue stand out more and more. The hues on either side of each of these actually *change,* gravitating toward whichever of the two is the nearer—that is, yellow and blue appear to spread more widely in the spectrum at the expense of their neighbors, until at very high intensities yellow and blue alone, greatly unsaturated, fill up the whole spectrum. At dazzling intensities even these lose all chroma and a sensation of whiteness is then evoked by any visible wavelength.

Yellow and blue thus appear unique in some respect. We shall see other aspects of their peculiarity shortly. It is important to note here only the fact that hue can be influenced by intensity. Apparently when the visual mechanism is being overworked, either its peripheral analytic or its central synthetic portion breaks down. We can change the hues that 'go with' particular wavelengths in still another way: by fatiguing the reception of a part of the spectrum we can make white light appear to consist only of the remainder of the spectrum, as in the production of 'complementary after-images'. More important, we can fatigue the synthetic mechanism itself, for if we stare for a time at a light which represents white-minus-red, and then look into a spectroscope, we will see not only the red where it 'belongs', but will see nearly the whole spectrum as red; and where there is no red (at the short-wave end) there is only darkness.* In the same way, green or violet can be made to spread out and fill almost the entirety of the spectrum, *but yellow and blue cannot be made to do so.* No better confirmation of our choice of red, green and violet as primary stimuli could be desired.

This phenomenon shows beyond question that whatever the three somethings may be which comprise the color-vision mechanism, each one of them has some responsiveness for practically all visible wavelengths. The results of fatiguing with colors show also that if each one of the somethings could be isolated and made to act all alone, its action would be to arouse a sensation of its appropriate primary hue, no matter what wavelength of light happened to activate it. Most of the 160-odd separate qualities we can experience, then, must be due to the instigation, by single wavelengths, of *combined* actions of the three processes, no one of which alone could give us more than a single, primary, hue sensation.

A rough idea of these combined actions is given by Figure 32. Each of the three colored curves represents the *spectrum of responsiveness* of one of the three central processes which synthesize our hue qualities, and the color of the line indicates the quality it arouses when allowed to act singly. When the redness and green-ness processes are equally active, the quality 'yellowness' results. When the green-ness and violet-ness

*The Ericksons have recently reported experiments which suggest that all 'fatiguing' for color may be central, rather than upon a peripheral exhaustion-of-photochemicals basis. Their hypnotized subjects 'saw' the proper complementary after-image colors after having had hallucinatory initial color-stimuli suggested to them; and these were persons who, in the waking state, did not know that there is such a thing as an after-image—let alone, that it should be expected to be complementary to the stimulus!

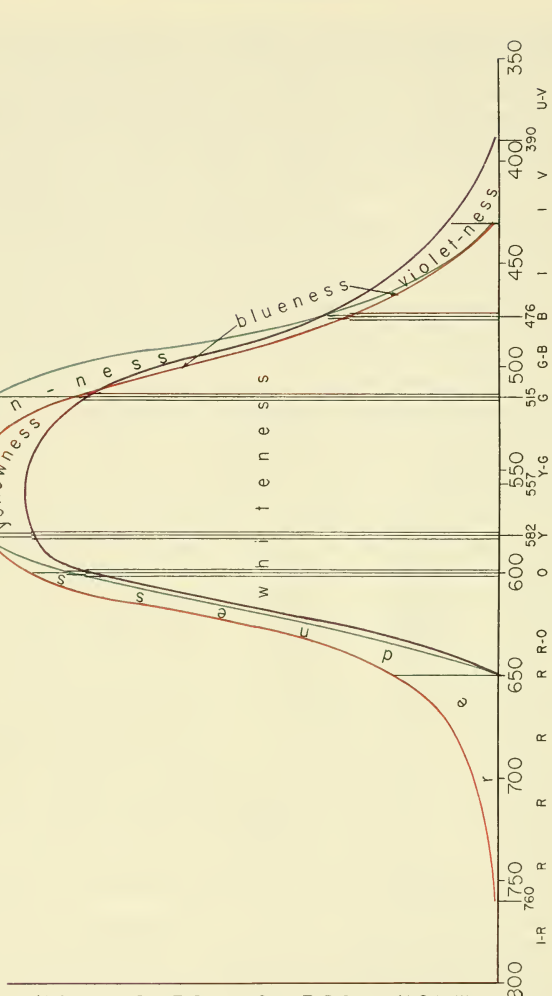

Fig. 32.—The three fundamental cerebral hue-sensory processes and their interaction in the synthesis of color sensations in normal trichromatic vision. So far as its ordinates are concerned, the graph is only very roughly quantitative. See full explanation in text.

processes are equal, the resulting sensation is 'blue'. When all three are equally activated (which of course cannot be brought about by any one wavelength) 'white' results.

At any one wavelength the ordinate, or height of the curves, has a heavy portion where it lies below all three curves. This represents equal amounts of activity of all three processes, and so represents the white valence, or unsaturating whiteness-component, of the sensation aroused by that wavelength. It needs of course to be given triple weight in any estimation of the relative whiteness- and chroma-contents of the various color sensations—their degrees of saturation. Above the triple line, the remainder of the ordinate represents chroma. The part of it which lies under two curves, taken twice, represents equal joint action of the processes represented by the two uppermost curves. At λ582mμ for example, the two uppermost curves cross and these processes are therefore equally aroused, yielding the compound sensation of yellow, diluted by a great deal of whiteness indicated by the heavy part of the ordinate lying below all three curves. Near the ends of the spectrum all of the ordinate represents chroma, which is another way of saying that these wavelengths are seen with complete saturation.

The unique character of yellow is now readily comprehensible from the graph. It results from the equal action of two processes which singly would yield respectively redness and green-ness, neither of which can be seen in yellow. Blue has a similar mode of origin—it is the unpredictable giraffe progeny of the horse of green and the zebra of violet. All of the sensation-qualities of mixed character except yellow and blue owe themselves to simpler blendings of sensation-components which, as with purple and orange, can still be discerned in the blend. The very names we use for mixed colors—bluish-red, reddish-yellow, and so forth —emphasize the simple character of their mixtures. On the other hand, no one would ever call yellow 'reddish-green', or blue 'greenish-violet'—and yet, in their genesis, that is what they are.

Let us consider just one of these mixed colors whose whole is merely the sum of its parts: orange. It will serve to exemplify the manner in which all such mixed colors are registered. At wavelength 600mμ in Figure 32, it will be seen that the double portion of the ordinate below the curve of the green-process is only half as tall as the part between the green and the red curves. But this part which is under the green curve is under the red curve as well, and hence is to be 'taken twice'. Moreover, it represents equal contributions of redness and green-ness to the

whole sensation aroused by λ600mμ—that is, a certain amount of yellowness. An equal amount of uncancelled redness still remains—the chroma ordinate above the green curve, taken once as to weight in the equation. At λ600mμ, then, the interaction of the three processes produces a large amount of whiteness and equal amounts of yellowness and redness. Such a blend, we see as orange.

Before we leave Figure 32 its representation of relative brightness and saturation need brief consideration. Brightness is most easily disposed of—as the reader has already gathered, it is represented by the total height of the variously-weighted portions of the ordinate. If each ordinate were drawn upward like an unfolding telescope to its 'true' height, the overall profile of the graph would represent exactly the curve of brightness of the photopic spectrum.

Saturation is maximal (100%!) at the ends of the spectrum—a fact which often goes unappreciated because of the low brightness of those regions and the confusion of brightness and saturation in the mind of the student. Saturation is always *the degree of freedom from admixture with white*, whether white external to the source of color is objectively added to the latter or not; for, the color itself, even if generated by a single wavelength, contains unsaturating whiteness as long as the wavelength in question sets off all three components of the central synthetic mechanism to any extents whatever. Under all ordinary circumstances we cannot have 'pure' colors, even in the spectroscope, without accepting an adulteration thereof by whiteness which arises from causes entirely within the central mechanism. In Figure 32, the intrinsic degree of saturation of any wavelength can be seen as the ratio of total chroma to whiteness, remembering to take singly the part of the ordinate from the topmost curve to the next one down, doubly the portion from that curve to the lowest, and triply the heavy line representing whiteness. It is obvious, however, that by fatiguing with the *complement* of a color we will so greatly reduce the height of the whiteness-ordinate that the saturation of the color will be correspondingly increased. Fatiguing with violet, for example, makes the yellow of the spectroscope—ordinarily the least saturated of all its hues—become amazingly rich in chroma; an experience never to be had otherwise, and never to be forgotten.

Color Blindness—'Color blindness' is an unfortunate term which includes at least five, perhaps six, kinds of departure from the normal trichromatic system. Total color blindness is the only type in which no

hues at all are seen, hence is the only type which should ever have been called color blindness at all. Vision is restricted to white, grays, and black, and the condition had best be called 'achromatic vision'. It seems nearly always to be due to the congenital absence, or a gross defectiveness, of the cones, for along with it there are usually to be seen: (*a*) low visual acuity both scotopically and photopically; (*b*) a central scotoma or blind spot where the bouquet of foveal cones should be; (*c*) a nystagmus or uncontrollable fluttering of the eyeballs owing to the lack of this central fixating region; and (*d*) photophobia or light-shyness, owing perhaps to an excess of rods, occupying the spaces where cones should be.

In 'anomalous trichromatic vision', some one spectral region appears less bright than it does to the normal person, and the individual requires more of such light, mixed with some other color, to match an intermediate color. An individual who, say, perceives green weakly must mix more green with less red than the normal individual, in order to match a standard yellow. This condition is not color *blindness*—it would much better be called color *weakness*.

These color-weak individuals have poor hue-discrimination and an increased perception-time for colors. They fatigue rapidly for colors, which seem to them to fade upon continued observation; and to identify some colors they require them in larger areas, with greater intensity and saturation, than the normal. Anomalous trichromates probably outnumber all other kinds of so-called color-blinds, but since they less often get into difficulty through unfortunate selections at the neckwear counter, they usually live and die without ever knowing of their peculiarity.

The conspicuous and familiar color-blind type is the dichromate or Daltonist, whose confusion of red and green is proverbial—and also hereditary, in a sex-linked fashion which keeps the defect a rare one in females. One white man in twenty-five is a dichromate, but only one white woman in twenty-five hundred. The dichromate is so called because he requires only two primaries, instead of three, to mix and match any and all hues and white. It so happens also that he can experience only *two* hues instead of the large number* of the normal trichromate; but the prefix (di = two) on his label does not refer to this latter fact. The dichromate is not color-*blind*—he is color-*poor*.

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*Usually taken as 160-180; but these are the discriminable hue-and-saturation complexes. Similarly, a dichromate can distinguish a large number (about 60) of spectral regions, but chiefly through saturation-differences.

The dichromate, in distinguishing most natural colors, must fall back upon saturation- and brightness-differences. The former are much the more important to him. Longwave colors look alike in hue to him, but very different in saturation. It is widely supposed, even by some expert psychologists, that a dichromate motorist tells red traffic signals from green ones on a basis of brightness, and is helpless to do so when bad weather dims them both. This is not the case. The brightness of the red and green lights could be varied up or down, or the red light made much brighter than the green (the reverse is usually true) without inverting his identifications; for the two lights would still retain their very different saturations.

For a long time, Daltonism was thought to be due to a literal absence of one of the three sets of receptors, or photochemical substances, or cerebral perceptual processes, of the Young-Helmholtz scheme of things. It was the physiologist Fick who showed, many years ago, that this could not be the explanation; but the lack-of-one-process theory is still taught far and wide. To adjust Figure 32 to represent dichromatic vision in accordance with Fick's contributions, none of the colored curves should be removed. It is only necessary to suppose that the spectrum of responsiveness of one of the three 'somethings' has shifted into coincidence with that of one of the other two.

To be specific, let us suppose that the redness curve is altered so that it superimposes upon the green-ness curve, and see what should inevitably result in the vision of the individual. Firstly, the spectrum would be shortened at the red end even in bright light. Secondly, redness and green-ness would always be contributed equally to the sensation evoked by all wavelengths from 650mμ to 476mμ. So, in this whole great spectral region the individual could see only *yellow* with varying degrees of saturation and brightness. He would have to learn to call the highly-saturated wavelengths red, and to call the less saturated ones yellow or green. Thirdly, from λ476mμ on to the ultra-violet, only violetness could be experienced, with saturation increasing as wavelength decreased. But his spectrum would contain something besides yellow and violet; for (fourthly) at λ476mμ all three processes would be in action to the same degree: *white* would result at this 'neutral point' in his spectrum. Fifthly and lastly, purple would not exist for him, for since redness and green-ness were inextricably tied together as yellowness in the long-wave part of the spectrum, the mixture of any wavelengths there, even those seen by the normal as red, with any of the wavelengths seen by

himself as 'violet', could yield only white since yellow and violet are complementary. For such an individual, proper amounts of any two wavelengths which were not on the same side of his neutral point could be mixed as complementaries to make white.

Now, the above is actually a fair description of one kind of dichromatic vision, called 'protanopia' in the older terminology since it was supposed to result from the lack of the first (protos = first) of the three component processes of trichromatic vision. Another, much more common, type is 'deuteranopia' (from deuteros = second). This form we can represent by shifting the green curve in Figure 32 to lie on top of the red one. The deuteranope experiences no shortening of the spectrum at the red end, and his neutral point is nearer the red end than that of the protanope (though neither of the actual neutral points is quite where it ought to be as theoretically called for by the diagram.) Otherwise, his experiences are about the same: two hues only, with one at either side of the neutral point; the same white region at the neutral point; and the same white or gray sensations from stimuli which appear to the normal as purple.

A condition much like dichromasy occurs, as a rarity, in one eye only. The individual is then able to tell us what he sees with that eye in terms of the trichromatic visual performance of his normal eye. Usually, he reports that the spectrum contains only yellow and *blue*, not violet as described above; but such pathological cases could not be expected to duplicate perfectly the situation in true Daltonism.

Theoretically, two other kinds of dichromasy are possible, but only one of them has been found (or else the two have been confused): 'tritanopia' is so extremely rare that it has not had proper study. We could represent its two possible versions by aligning the green curve of Figure 32 with the violet, or the violet curve with the green one. The tritanope's neutral point, depending, would then coincide with either the protanopic or deuteranopic one. In the latter case, the spectrum would be shortened at the violet end. In either case, the only possible hue-experiences, it would seem, would be red and blue. The shortened spectrum of at least some tritanopes seems to have been noticed by the older investigators and recognized in the common name of the condition, 'blue-blindness'. Tritanopia can be simulated in some individuals by excessive absorption of short-wave light in an abnormally rich macular pigmentation (see Chapter 8, section D), or in an extremely yellow, pre-cataractous lens; and also by the yellowing of vision in jaundice

(usually ascribed to tinting of the vitreous by bilirubin—but E. Sachs finds no such yellowing in icteric dogs; perhaps the *retina* is colored).

Photochemistry of Color Vision—So much as to suggestions regarding what goes on in the higher reaches of the chromatic visual mechanism. Now, what objective realities can we point to, in the way of a physiological mechanism for analyzing and transmitting assortments of wavelengths in and from the eye? Sadly, only one dubious photochemical substance of ambiguous properties.

In 1930, Gotthilft von Studnitz reported the first revelation of a retinal photochemical since the discovery of Boll and Kühne. Studnitz has never given the material a real name—it is just the 'Zapfensubstanz' (*i.e.*, cone-substance). Several years later Wald in this country, without reference to Studnitz's work, hypothesized a cone substance which he named iodopsin (iodos = violet) on the assumption that if one could isolate and concentrate it, it would be found to be violet in color. 'Iodopsin', however, was based upon technical methods which Studnitz has ever since insisted could not possibly have indicated his own zapfensubstanz, but rather involved a serious error on Wald's part. Studnitz has consequently refrained from applying Wald's appropriate name to the substance which he has claimed to be able to extract and study. For any detailed discussion of the zapfensubstanz, the reader must go to the work of Studnitz cited in the bibliography. No one outside of his group has worked on the substance in all the years since its announcement. Remarks on it here will be brief.

Studnitz first identified this photosensitive substance by comparing the capacity of a fresh retina for absorbing light, before and after being exposed to strong light. After such exposure, the retina was found to be more transparent than before, which could apparently only be the result of the destruction of some photosensitive substance. The first retinæ employed were duplex; so, to eliminate rhodopsin from the picture, Studnitz repeated his experiments on some pure-cone retinæ. Here also he found the substance, which therefore must be in the cones. He learned how to study it by itself in rhodopsin-bearing retinæ, though not how to isolate its effects very well from those of cone oil-droplet pigments, which come out in the same solvents and are slightly photosensitive.

By comparing the change, before and after the bleaching with strong light, in the amount of various monochromatic lights absorbed, Studnitz was enabled to plot a curve of the absorption spectrum of the zapfen-

substanz; and this curve eventually received complete confirmation when he obtained the absorption spectrum of the compound isolated from the retina by extraction with ether and chloroform. Extracts of fish, frog, turtle, and mammalian material contained various, always tiny, amounts of the material whose maximum absorption of light was invariably at λ560mμ or thereabouts—the position of the peak of the photopic brightness curve, just as the peak of absorption of rhodopsin coincides with the bright spot in the scotopic spectrum (Fig. 34; *cf.* Fig. 33).

In fact, the absorption spectrum of the zapfensubstanz proved to be superimposible over the photopic brightness curve, after some alterations which lay Studnitz open to the serious charge of 'wangling'.

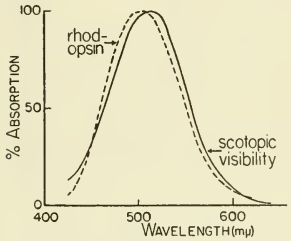

Fig. 33—Similarity of the graph of the absorption spectrum of rhodopsin (frog) and that of the luminosity of the spectrum to the scotopic human eye. Redrawn from Grundfest.

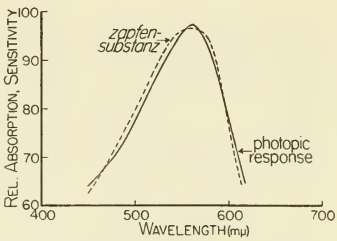

Fig. 34—Similarity of the graph of the supposed absorption spectrum of the photochemical material of the cones, and that of the electrical responsivity of the photopic retina through a portion of the photopic spectrum (here taken as indicative of photopic luminosities). Redrawn from von Studnitz.

Herein lies the chief claim of the zapfensubstanz to acceptance as the essential photochemical of cone vision—and, at the same time, its most puzzling quality when the Young-Helmholtz theory is kept in mind. It is very nice to hear at last that there really is an extractible photochemical substance in the vertebrate cone visual cell. It is not so convenient to find that this one substance, single-handedly, appears capable of accounting for the whole of the photopic brightness curve. There ought to be *three* zapfensubstanzes, the overall profile of whose absorption spectra would just neatly fill out all the corners under that curve! Studnitz, indeed, recognizes the possibility that what he has called one substance is really a group of three which his solvents cannot separate from each other. In fact his very latest curves, derived from snake

material, show *three* peaks instead of one. He thinks the precursor of the substance is the carotenoid pigment of the cones' oil-droplets (for this there is no evidence whatever) and points out that the multiplicity of such pigments in turtles and birds suggests that several different photochemicals, à la the multi-component color-vision theories, are formed from them. How this works out in the lizard, which sees all colors and yet has only yellow pigment in its oil-droplets—or in man, who has no oil-droplets at all (see Chapter 8, section D), Studnitz does not tell us.

So far, then, we are told of but the one substance. Its very existence is most dubious, for leading authorities are very skeptical of Studnitz's

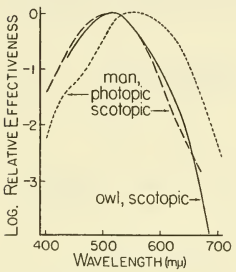

Fig. 35—The Purkinje shift as shown by the relative brightnesses of monochromatic lights to the photopic and scotopic human eye. Also, the relative pupil-closing effectiveness of monochromatic lights upon the scotopic eye of an owl, *Asio wilsonianus*. Redrawn from Hecht and Pirenne.

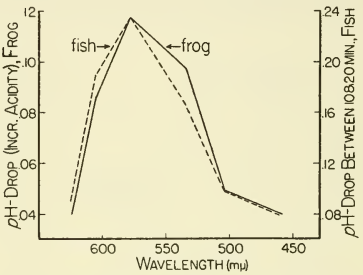

Fig. 36—Formation of acid (phosphoric?) in retinæ under monochromatic light—supposedly owing to breakdown of the cones' photosensitive material, and showing similarity to graphs of photopic brightnesses. Redrawn from von Studnitz.

claims and critical of his methods. Granting that Studnitz has really found a cone-substance—it may really be three, but if so we know not how to separate them. Its precursor is quite unknown; but its end-product upon breakdown under light is supposed to be phosphoric acid (Fig. 36). When we try to understand the retinal part of the physiology of color vision, a single zapfensubstanz seems more of a hindrance than a help. And if we choose rather to believe in the solitary 'iodopsin' of Wald and Chase, we are no better off. Different wavelengths would break down different amounts of the whole concentration of the substance, and we can easily imagine that corresponding kinds of optic nerve impulses—differing in modulation or whatnot—are produced and

then integrated centrally where they set off the respective three component processes of the synthetic mechanism. But, for any one wavelength there is another on the other side of the peak of the absorption spectrum of the zapfensubstanz, which at the same intensity would break down the same amount of the substance into, presumably, the same end products. How then could these two wavelengths possibly arouse different sensations? It is impossible to imagine how any one substance could serve as the analytical mechanism by which purple light is translated into 'redness modulated' and 'violet-ness modulated' impulses in a single optic nerve fiber. For the cones to generate three qualitatively different impulses, it would appear that they must contain a triplex photochemical system.

In truth, the working out of the photochemical system of the cone may long continue to seem the most difficult branch of the physiology of the eye. To absorb more light in one part of the visible spectrum than another, a substance must be colored. In the present state of our knowledge we must suppose that there are tiny amounts of three differently-colored photosensitive substances in the cone's outer segment. With the very sloppiest of technique, we can mount the fresh dark-adapted retina of a frog or a goldfish on the microscope and still see the rich wine of rhodopsin filling its rods. But with the most careful of methods, we can succeed in seeing living cones only as completely colorless structures, whose bland innocence conceals invisible traces of three important somethings—to our utter exasperation.

Chapter 5

THE GENESIS OF THE VERTEBRATE EYE

(A) Embryological

There are many anatomical relationships in the eye which are extremely puzzling when we look only at their adult condition, but which become perfectly clear if we follow their ontogeny. A little knowledge of the embryonic development of the eye is therefore highly desirable. The process is a fascinating one in its own right, but we shall examine it here as a means to two ends: the embryology of the eye can be expected to shed some light upon its evolutionary origin; and, the developmental scheme serves as a framework within which all possible adaptive evolutionary changes of ocular structure must fit. If we know how the eye develops we can guess where it came from, we can see how it has been able to take on the modifications which fit it for greater efficiency in this or that environment, and we can see why it has not been able to make some changes that might seem to us more logical than particular ones which it has happened to accomplish.

The following account is a generalized one which applies in its entirety to no particular animal, but is based upon the mammals because their story is known in the greatest detail. Some important departures characteristic of other vertebrate classes will be pointed out specifically, but in general the reader who wishes to imagine the ocular embryology of a lower class needs only to make a mental subtraction, from the mammalian process, of those features which the lower group lacks, in order to have a fairly accurate conception.

The parts of the eye are recruited from three sources in the embryo: (*a*) the ectoderm of the neural tube, which is in turn derived by infolding from the surface ectoderm and which later differentiates into the brain and spinal cord; (*b*) the surface ectoderm remaining after the neural tube has been formed and separated from it; and (*c*) the mesoderm lying between the neural tube and the surface ectoderm.

Formation of the Optic Cup—These three sources start to make their respective contributions in this same order. The brain being by far the most complex organ in the body, it begins to develop before any other; and the eye gets an equally precocious start since its most essen-

tial part, the retina, is a derivative of the neural tube. Even while the tube is still an unclosed groove in the surface ectoderm, the beginnings of the two retinæ can be seen as a pair of dimples in the anterior portion of its floor—the part destined to become the forebrain of the embryo.

As the lips of the neural groove approximate and fuse to close the neural tube and push it beneath the surface ectoderm, these pits or 'foveolæ opticæ' (Fig. 37a) are each rotated through a right angle so that they form a pair of bumps on the sides of the closed-in forebrain (Fig. 37b). They rapidly expand as if blown up from the inside, and each becomes a bubble of tissue attached to the side wall of the forebrain by a broad, very short, hollow stalk.

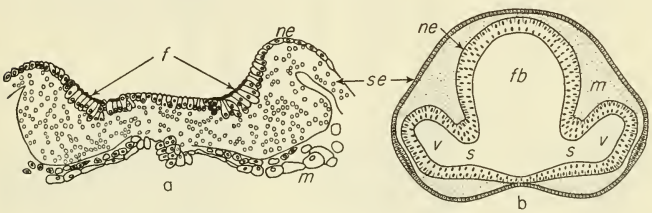

Fig. 37—Formation of the optic vesicles.

a, cross section of anterior portion of frog neural groove, as yet unclosed, showing foveolæ opticæ. Redrawn from Eyclesheimer.

b, cross section of head of 4mm. human embryo, after closure of the neural groove—the foveolæ now form the optic vesicles. Redrawn from Mann.

f- foveolæ opticæ; *fb*- embryonic forebrain; *m*- mesoderm; *ne*- neural ectoderm; *s*- optic stalk; *se*- surface ectoderm; *v*- optic vesicle.

At this stage the bubble of forebrain tissue is in contact with the surface ectoderm of the side of the head and is known as the optic vesicle, its connection with the forebrain proper being called the optic stalk. The stalk slowly shifts its root backward as the brain becomes serially constricted into five chambers, and is eventually connected with the second of these, the diencephalon or tween-brain.

Two processes now set in, one in the optic vesicle and one in the surface ectoderm, which go on simultaneously and look superficially as though one of them must be causing the other: an indentation of the optic vesicle to form a two-layered optic cup; and an in-sinking of a portion of the surface ectoderm to form a closed hollow ball of tissue. the lens vesicle, which comes to lie in the cavity of the optic cup. The

formation of the lens vesicle *is* absolutely dependent upon the presence of the optic vesicle against the surface ectoderm—but not in any mechanical way: the lens-organizing influence of the optic vesicle is exerted chemically. If the optic vesicle is removed, no lens vesicle is

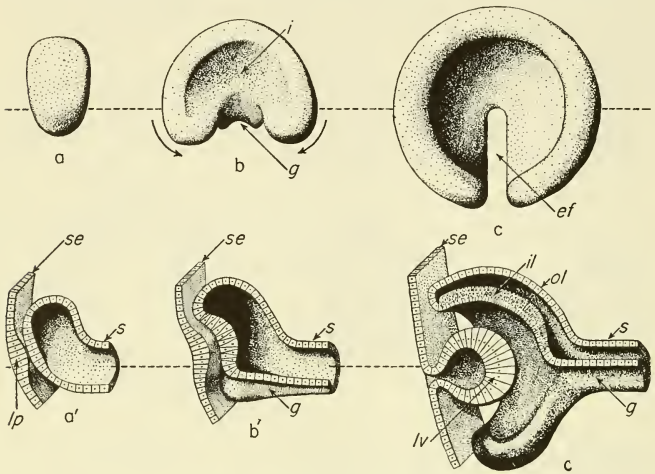

Fig. 38—Formation of the optic cup.

a, b, c, diagrammatic models of optic vesicle, transitional stage, and completed cup as seen from the side of the embryonic head with the surface ectoderm removed. The curved arrows in b show the direction of growth of the lateral portions of the vesicle which, while the indentation of the face of the vesicle is taking place, grow below the level of the axis of the optic stalk (dotted line) to form the ventral half of the cup. The embryonic fissure is created by the temporary failure of the down-growing lobes to meet and fuse.

a', b', c', optical sections through the stalk axis (dotted line), corresponding respectively to a, b, *and* c. A patch of surface ectoderm has been left in place to show the development of the lens vesicle.

ef- embryonic fissure of optic cup; *g*- groove on underside of optic stalk (continuation of embryonic fissure); *i*- invagination of face of vesicle; *il*- inner layer of optic cup (future retina); *lp*- lens placode; *lv*- lens vesicle; *ol*- outer layer of optic cup (future pigment epithelium); *s*- stalk; *se*- surface ectoderm.

formed; and if the optic vesicle is planted under any other surface ectoderm, even on the belly of the embryo, a lens vesicle will proceed to form from that ectoderm. Similarly, if the developing lens vesicle is removed, the optic vesicle goes right ahead with its indentation—the latter is an active process, not caused mechanically by the inward pres-

sure of the developing lens; nor is the surface ectoderm passively sucked inward, to form the lens vesicle, by the cupping of the optic vesicle.

The conversion of the optic vesicle into the optic cup is more than a simple indentation or invagination (Fig. 38). At first, the dilated vesicle lies largely above the level of the optic stalk, but after the completion of the optic cup the stalk is found to be attached to the center of its back. Figure 38b shows what really happens—a growth of the two sides of the base of the vesicle laterally and downward, closing in below the attachment of the stalk. The closure is not at first complete, so that a slit, the 'embryonic fissure of the optic cup' is left in the ventral

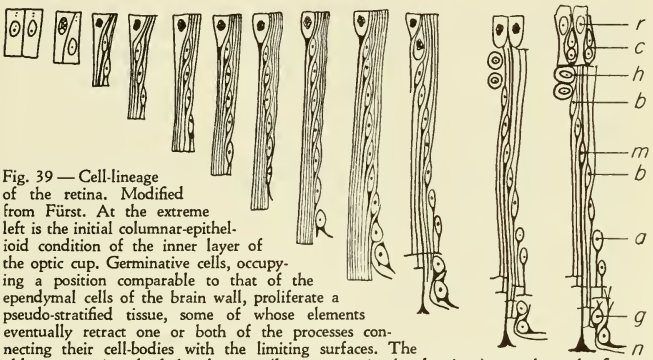

Fig. 39 — Cell-lineage of the retina. Modified from Fürst. At the extreme left is the initial columnar-epithelioid condition of the inner layer of the optic cup. Germinative cells, occupying a position comparable to that of the ependymal cells of the brain wall, proliferate a pseudo-stratified tissue, some of whose elements eventually retract one or both of the processes connecting their cell-bodies with the limiting surfaces. The oldest, most vitread of the elements (bottom-most in the drawings) are about the first to differentiate, and maturation proceeds outward toward the germinative cells, which at last become the rods and cones.

r- portion of rod; *c*- cone; *h*- horizontal cell; *m*- Müller fiber; *b, b*- bipolar neurons; *a*- amacrine cell; *g*- body of ganglion cell; *n*- nerve fiber (axon of ganglion cell).

meridian of the cup, running from its rim to the cup end of the optic stalk. Along the under side of the stalk, nearly all the way to the brain wall, there is now a deep groove which has invaginated during the formation of the optic cup. This groove opens into the cavity of the optic cup and here forms the apex of the embryonic fissure. The old cavity of the optic vesicle has been nearly obliterated by the indentation of the vesicle. It, through its continuation in the optic stalk, still opens into the forebrain cavity but of course has no communication with the new cavity of the optic cup or with that cavity's continuation, the ventral groove of the optic stalk.

Differentiation of the Retina—The optic cup now has two layers of tissue in its wall whereas the optic vesicle had but one (Fig. 38c', *il, ol*). The outermost of these layers remains forever one cell thick and its cells shortly develop pigment granules, the whole layer becoming eventually the pigment epithelium of the retina. The cells of the inner layer of the optic cup rapidly proliferate, forming many layers from which will be derived the various layers of the adult sensory retina (Fig. 39). Since it is the outermost of these cells (toward the pigment epithelium) which are multiplying, their daughter cells are pushed ever inward toward the cavity of the optic cup. It follows that these innermost cells are the oldest at any one time and they are naturally the first to differentiate. They lie in the position of the ganglion cells of the adult retina; and it is into these that they develop, soon protruding their axon fibers which grow along the inner surface of the optic cup. These fibers all aim for the cup end of the optic stalk—the site of the future disc—and here turn outward and grow down through the tissue of the stalk (*not* through the groove on its under side) to make their connections in the wall of the diencephalon. They form the optic nerve fibers; and a few cells of the stalk tissue, which escape destruction by them, proliferate the neuroglial cells which help to form the system of interfascicular septa in the adult nerve.

The further differentiation of the cells of the inner layer of the optic cup proceeds in a two-fold manner: from the inner surface toward the outer (next the pigment epithelium) and from the posterior pole of the cup forward along all meridians toward the rim. At the posterior pole, the future amacrine cells can be recognized soon after the ganglion cells and Müller fibers have differentiated. The bipolars and horizontal cells next become distinguishable; and, when proliferation finally ceases, the cells nearest the pigment epithelium (which have been doing the proliferating) are finally free to differentiate into the rods and cones—the last elements in the retina to mature though they are the most ancient cells in the eye and are its whole reason for being.

At any one time, these changes are further advanced at the posterior pole than they are out toward the rim of the cup, where cell-division may still be seen long after it has ceased in the fundus of the retina. The optic cup thus grows at its lip, and rapidly increases manyfold in diameter and in surface area as the embryo enlarges. A convenient consequence of this is that it is possible to study the whole process of retinal differentiation in a single favorable section of a single embryonic eye,

simply by examining regions which are successively farther from the posterior pole and nearer to the ora terminalis, or rim of the cup. Another consequence is that the region of the ora is to some extent permanently juvenile. If the retina is destroyed and subsequently regenerates (as it will do in amphibians, though not in any other vertebrates) the new retina grows from the ora terminalis, creeping backward until the fundus is filled; and a new optic nerve develops *pari passu* with the regeneration. A perennial mystery, however, is the fact that the retina continues to increase greatly in extent after all cell-division has apparently ceased in it—as is the case, for instance, in an amphibian which is on the verge of metamorphosis, though the eye is then nowhere nearly adult in size. It is possible that sensory-retinal elements continue to differentiate from the ciliary epithelial cells (*v.i.*) at the ora, and the application of the colchicine technique may solve this problem.

The Lens—All this time, the lens has been developing. Commencing as a local thickening in the surface ectoderm, the 'lens placode' evoked by some chemical emanation from the contiguous optic vesicle, it has invaginated and pinched free of the surface ectoderm, which heals over it without trace.

Thus is formed the lens vesicle, lying in the mouth of the optic cup (Fig. 38c′). Its posterior or inner wall rapidly thickens, each of the cuboidal cells becoming columnar and continuing to elongate until it is a slender fiber. The growth in length of these cells being in a forward direction, they encroach upon the cavity of the lens vesicle and obliterate it, forming a solid mass whose anterior surface is still covered over by the unmodified cuboidal cells of the original anterior wall of the vesicle (Fig. 40). This cuboidal layer is the lens epithelium, and at the equator of the lens it forever remains continuous with the greatly thickened posterior wall. In this region of transition, epithelial cells now commence to elongate and to rotate their axes of polarity until they are no longer radially oriented with respect to the center of the lens, but circumferentially disposed (Fig. 41a). The two ends of these elongating equatorial cells disconnect from the ends of their neighbors in the epithelium and grow apace, one end sliding forward under the epithelium and the other end backward, guided by the confining capsule which has already been secreted by the lens vesicle over its whole outer surface.

Thus a layer of circumferential lens fibers is laid down, like one of the skins of an onion, over the central mass of original, straight lens

fibers which were formed directly from the cells of the posterior wall of the lens vesicle. The further conversion of crop after crop of cuboidal epithelial cells, at the equator of the lens, results in layer after layer of fibers each of which is added outside of the previous one (Fig. 41b). Any one fiber being too short to stretch from pole to pole of the lens, its anterior and posterior ends meet, head-on, the corresponding ends

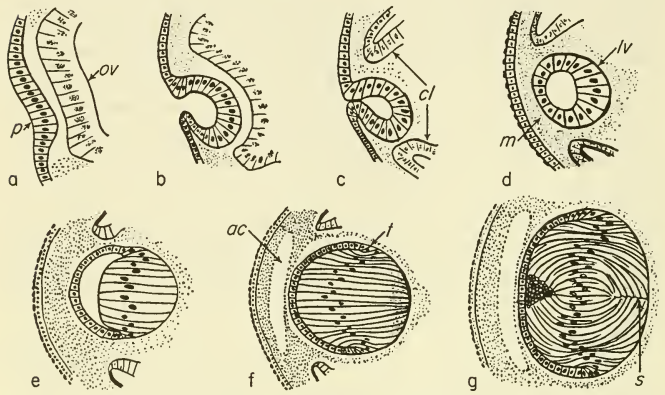

Fig. 40—Early stages of the lens. Redrawn from Mann.

a, placode stage, comparable with Figure 38a'; *p-* lens placode formed in surface ectoderm; *ov-* optic vesicle. b, c, lens pit forming and closing off; *cl-* lips of optic cup. d, lens vesicle has detached and passed into mouth of optic cup; *lv-* lens vesicle; *m-* mesenchyme which has now invaded space between optic cup and surface ectoderm. e, cavity of lens vesicle being obliterated by the elongation of the posterior wall cells to form the first of the lens fibers. f, lens is now solid, and its present fiber mass will constitute the 'embryonic nucleus' of later life (*cf.* Fig. 41b); *t-* zone of transition of epithelium into fibers—the locus at which all future fibers will form; *ac-* anterior chamber forming as a cleft in the mesoderm, separating the latter into the future cornea and the future iris stroma. g, new fibers have been added to the embryonic nucleus and are meeting end-to-end at anterior and posterior suture planes; *s-* posterior suture (*cf.* Fig. 41b, *sp*).

of a diametrically opposite fiber. These meeting points are aligned in radial planes within the lens mass, called lens sutures (Figs. 40g, 41b and c), which perforce branch more and more toward the surface of the growing lens as the number of epithelial cells ringing the equator increases and the number of fibers seeking place for their tips against the suture planes increases. At any one time, there are many superficial layers in which the fibers have not yet elongated enough to reach suture

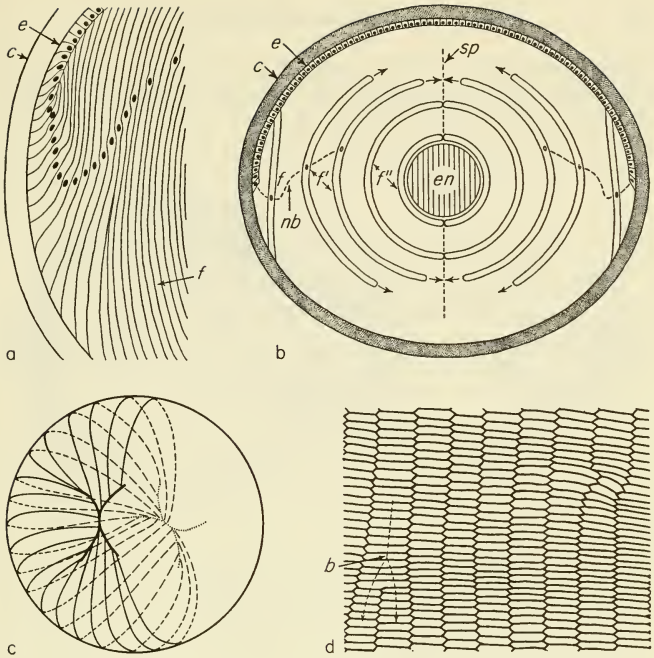

Fig. 41—Growth of the lens.

a, diagram of the equatorial region of a growing lens, showing how the cells of the lens epithelium, *e*, elongate and reorient their axes of polarity to convert into lens fibers, *f*, whose ends slide forward under the epithelium and backward under the capsule, *c*, as they take on a circumferential course.

b, diagram showing growth of lens fibers; the youngest, in the vicinity of *f*, are still in contact with the epithelium *e* and capsule *c* (*cf.* **a**). *f'*- cortical fibers which are still growing as indicated by the arrows, and have not yet reached suture planes. Their nuclei, distributed along the nuclear bow *nb*, slowly fade as the fibers gradually sclerose upon being marooned in the heart of the lens by the addition of newer fibers peripheral to them. Oldest, hardest fibers of all are those of the 'embryonic nucleus' *en*, formed directly from the posterior wall of the lens vesicle (*cf.* Fig. 40). *f''*- fibers which have reached the suture plane *sp*. (All fibers in the section are shown as if in one plane—actually, they spiral so that the suture planes of the front and back halves of the lens are at right angles; *cf.* **c**).

c, superficial fibers of the adolescent nucleus of the human lens, showing the 'lens stars' which represent the intersections of the branched suture planes with the surface. Redrawn from Mann.

d, portion of equatorial section of human lens, showing radial lamellæ of lens fibers and the hexagonal shape of the latter in cross section. ×500. From Maximow and Bloom, after Schaffer. *b*- branching of a radial lamella, which occurs repeatedly as the equatorial perimeter of the lens enlarges during growth. (All the fibers shown in **a** lie in one radial lamella).

planes, creating an unsutured cortex overlying a sutured core, the cortex becoming proportionately thinner as the lens ages and the rate of fiber-formation is slowed (see also pp. 20-1).

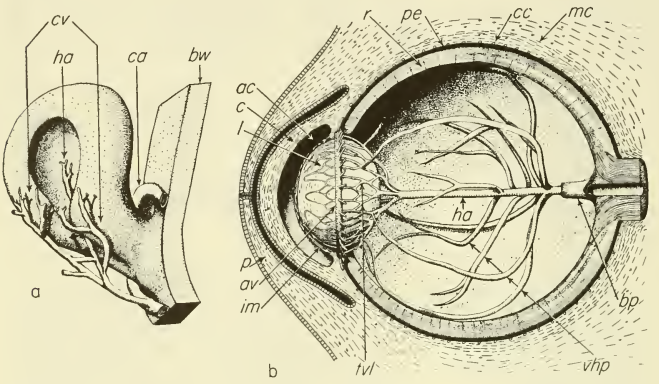

Fig. 42—The hyaloid circulation.

a, model of invaginating mammalian optic vesicle, showing future hyaloid artery being taken up through the embryonic fissure. Based upon figures of Mann.

bw- brain wall; *ca-* carotid artery; *cv-* first chorioidal vessels, which will anastamose around cup rim to form the annular vessel, and will branch over cup surface to lay down the choriocapillaris; *ha-* hyaloid artery.

b, model of fetal mammalian eye in optical section, showing the hyaloid system at the peak of its development. Based upon figures of Versari.

ac- anterior chamber; *av-* annular vessel; *bp-* Bergmeister's papilla (neuroglial support at base of hyaloid, which will later atrophy with the hyaloid vessels, leaving a cup in the nerve head); *c-* cornea; *cc-* choriocapillaris (first vessels of the chorioid to form); *ha-* trunk of hyaloid artery, traversing vitreous cavity; *im-* iris mesoderm, containing capillary arcades thrown forward from annular vessel; *l-* lens; *mc-* mesenchymal (mesodermal) condensation which will form chorioid and sclera; *p-* lids (temporarily fused over cornea); *pe-* pigment epithelium of retina; *r-* retina, with neuroblastic layer still single anteriorly but already divided into inner and outer layers in the precocious fundal region; *tvl-* vessels of tunica vasculosa lentis, encapsulating the growing lens; *vhp-* vasa hyaloidea propria, supplying the vitreous and the retinal surface—the last vessels of the system to differentiate, and usually the first to atrophy.

This growth process never completely stops until death, though it is greatly retarded after the eye has reached its adult size. The oldest fibers of the lens being the innermost ones, it is these which first feel the effects of being removed farther and farther from any possible source of food and oxygen, and they sclerose (harden) and die. The sclerosis involves

more and more outlying layers of fibers until the dead, firm centrum of the lens has grown in size (by middle age) to the point where little accommodatory change of shape of the lens is any longer possible (see Fig. 15, p. 35). The lens is thus unique among the organs of the body in that its development never ceases, while its senescence commences even before birth.

The Hyaloid Circulation—In mammals, though not in any other class, the developing lens is nourished by an elaborate temporary network of blood vessels. The first signs of their development are seen while the optic cup is just being formed. From a plexus of embryonic capillaries lying beneath the vesicle, one especially plump vessel is taken up into the groove of the optic stalk (Fig. 42a) so that when the lips of this groove finally close, the little vessel lies along the axis of the future optic nerve and forms the 'hyaloid artery'. At the optic-cup end of the groove of the optic stalk, it emerges into the cup cavity. The healing of the embryonic fissure of the optic cup fixes the point of emergence of the hyaloid artery at the site of the apex of the fissure. As it traverses the vitreous cavity it branches around the lens to form a vascular tunic on the latter, and some of these branches make connections at the rim of the optic cup with other vessels clinging to the outer surface of the cup, the beginnings of the chorioidal circulation. A ring-shaped 'annular vessel' is formed at the cup margin, and from it capillary loops are thrown over the anterior face of the lens, budding through the mesodermal tissue which has squeezed in between the lens and the surface ectoderm, and thus laying down the circulation of the embryonic iris (Fig. 42b).

The whole vascular net around the lens, the other branches of the hyaloid artery which run along the inner surface of the retina, and the hyaloid artery itself eventually (before birth) atrophy back to the head of the optic nerve. Here the hyaloid (now called the central retinal artery) gives off new branches into the retinal tissue, accompanied by branches of the central retinal vein, to give the retina its definitive circulation.

The Vitreous—In among these temporary vessels in the cavity of the young optic cup there is a gelatinous tissue, the 'primary vitreous', whose few fibers are of dual origin, some being produced by mesodermal cells which invaded the cup with the hyaloid vessel, others coming from the foot-plates of the Müller fibers of the developing retina, and even from the cells of the lens until the formation of the capsule shuts off further

contributions. Most of the definitive or secondary vitreous is secreted by the retina during the growth of the eye, the primary vitreous coming to form a slender cone with its base on the back of the lens and its apex at the head of the optic nerve (Fig. 43). The final disappearance, from this primary vitreous, of the last remnants of the hyaloid circulation leaves it in the form of a conical tube (filled with vitreous thinner than

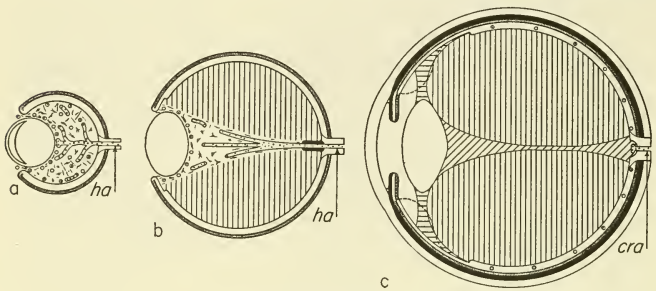

Fig. 43—Formation of the vitreous.

a, diagrammatic section of young optic cup showing vessels of the hyaloid system embedded in the primary vitreous, consisting of mesodermal fibers and cells (which invaded the cup along with the hyaloid artery *ha*), together with fibrils secreted by the ectoderm of the cup, lens, and surface.

b, diagrammatic section of fetal optic cup in which atrophy of the vasa hyaloidea propria (*cf.* Fig. 42b) has clarified the peripheral vitreous, to which has now been added much secondary vitreous (vertical hatching) secreted by the sensory retina. The persisting tunica vasculosa lentis and the trunk of the hyaloid artery *ha* are embedded in a cone of primary vitreous.

c, the definitive situation (*cf.* Fig. 3, p. 7): the canal of Cloquet represents the remnants of the primary vitreous, stretched to a slender column by the growth of the eye (diagonal hatching). The secondary vitreous (vertical hatching) nearly fills the globe. The tertiary vitreous (horizontal hatching) is constituted by the fibers of the zonule, secreted lastly by the non-sensory retina. The optic-nerve portion of the hyaloid artery alone persists, as the central retinal artery *cra*, and has given off new branches into the retinal tissue.

the secondary kind), the canal of Cloquet. This canal runs through the vitreous from disc to lens in the adult, with a considerable sag along its course caused by gravity and time (see Fig. 3, p. 7).

The Vascular and Fibrous Tunics—As soon as pigment granules appear in the outer layer of the finished optic cup, a network of capillaries—the future choriocapillaris—is formed in the mesoderm against the pigment epithelium. Larger vessels developing outside of these, and

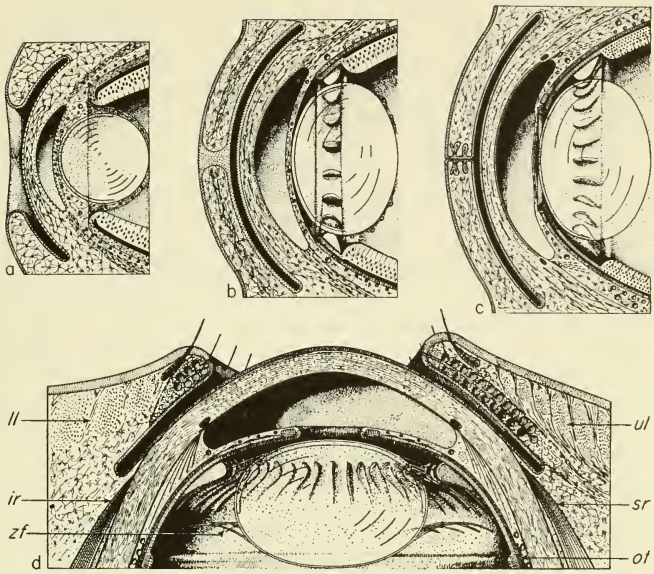

Fig. 44—Formation of the anterior segment (modeled in optical section, based upon the process in primates; scale decreases from a to d).

a, young embryo (*cf.* Fig. 40f). Anterior chamber has formed; lids closing over cornea; scleral condensation has appeared.

b, advanced embryo. Chamber is broader; lids are fused by epithelial plug; cornea has stratified epithelium, mesothelial lining; back wall of chamber still wholly mesodermal, but optic cup margin has put forth a thin outgrowth bearing meridional ridges (ciliary processes); major circle of iris can be made out.

c, fetus. Chamber still broader, its margin nearer to major circle; lids still fused but with lash follicles, Meibomian and other glands budding in from ectoderm; Descemet's membrane and canal of Schlemm formed; ciliary muscle and large-vessel layer of chorioid taking shape; hyaloid system has degenerated; continued forward growth of optic cup margin (leaving corona ciliaris behind) has given the iris mesoderm its ectodermal backing (from which the sphincter is differentiating) but leaves a thin film of mesoderm over the lens—the pupillary membrane, which will soon atrophy.

d, fetus near term. Chamber will broaden yet more, well past Schlemm's canal; lids reopened and well differentiated; cornea and anterior sclera fibrous; rectus muscles formed; ciliary muscle fully developed; iris complete—dilatator differentiated, pupillary membrane gone; formerly narrow zone between original optic cup margin and precociously-formed corona now greatly expanded, creating orbiculus ciliaris and leaving old cup margin far behind as the ora terminalis; zonule fibers, growing out from orbiculus, have attached to lens capsule.

ir- inferior rectus; *ll*- lower lid; *ot*- ora terminalis; *sr*- superior rectus; *ul*- upper lid; *zf*- zonule fibers.

connected with them, become the arteries and veins of the chorioid coat. The mesoderm around the optic cup condenses to form the connective-tissue substrate of the chorioid and sclera, at first one mass but later separated by the formation of the epichorioidal lymph-spaces. Other early mesodermal condensations develop into the extra-ocular muscles and other orbital contents.

The anterior chamber is formed quite early as a cleft in the mesoderm between the lens and the surface ectoderm, separating this mesoderm into that of the iris and that of the cornea (Fig. 40, *ac*; Fig. 44). The two layers may become neat and regular even before their separation. The corneal mesoderm differentiates into the substantia propria, and the overlying surface ectoderm contributes the corneal epithelium. The lining cells of the embryonic anterior chamber become the latter's mesothelium, secreting (on the inner side of the cornea) Descemet's membrane as their basement membrane.

The iris is thus at first wholly mesodermal, and there is no aperture in it, the future pupil being filled in by a mesodermal 'pupillary membrane' which must later atrophy. The two ectodermal layers of epithelium on the posterior surface of the iris are laid down by the optic cup in the following way:

The thick rim of the optic cup, the future ora terminalis of the sensory retina, suddenly resumes proliferation, and a bud-like prolongation of it creeps out under the mesoderm of the iris, between that mesoderm and the lens, forming a thin double epithelium whose two layers are respective continuations of the pigment epithelium and the retina proper. This is actually new growth, for the optic cup proper does not expand to accomplish it, as is evidenced by the fact that the original thick rim 'stays put'. The first structure laid down by this thin anterior continuation of the cup lip is the future corona ciliaris; but when this has been produced the growing lip does not stop, but cuts through the vitreous which is joined to the root of the iris and continues out under the iridic mesoderm as far as the site of the future pupil margin, leaving the pupillary membrane devoid of an ectodermal backing.

The outer layer of this epithelial fold is pigmented like the retinal pigment epithelium of which it is a continuation, and during its growth the pigmentation begins also to involve the inner layer of cells, creeping backward from the growing lip as far as the root of the iris, where it stops. This leaves the innermost of the two layers of epithelium which cover the ciliary body forever free of pigment granules, forming the

ciliary epithelium. In the iris, the outer or anteriormost of the two layers of epithelial cells eventually loses much of its pigment (*cf.* Fig. 7g, p. 15) as it gives rise to the sphincter and dilatator of the pupil, which are thus the only ectodermal muscles in the body.

In the ciliary body, mesodermal cells differentiate into the ciliary muscle fibers, and the anterior chamber widens and deepens greatly through the erosion of tissue at the iris angle. From the ciliary epithelium there develop the cuticular fibers of the suspensory ligament or zonule, which are regarded collectively as the tertiary vitreous and which grow axiad to gain secondary attachments to the lens capsule. The anterior surface of the secondary vitreous then drops back to its definitive position, its surface presented to the aqueous forming the anterior hyaloid membrane; and the aqueous of the anterior chamber is free to spread back into the posterior chamber and the canal of Hannover. With the formation of the zonule, the main features of the eyeball are established.

Lids and Glands—The lids arise as a circular fold of skin around the front of the eye which closes in over the cornea, with its circular aperture rapidly becoming a horizontal slit, thereby creating upper and lower lids. The margins of these fuse together early in fetal life, opening again much later—from a few days to six weeks after birth in mammals which are born hairless and helpless. The time of reopening always coincides closely with that at which the rods and cones have finished their differentiation. That differentiation, it is interesting to note, can be speeded up a couple of hundred percent by surgically opening the lids of the newborn mammal and keeping it and its mother in a lighted place. The various glands of the lids, the lacrimal and Harderian glands, and the lacrimal drainage system are all ectodermal derivatives; but their mode of development is unimportant to us here.

Variations in Non-Mammals—Some major departures from the above process, which occur in the different vertebrate groups, are mentioned briefly below and will be dealt with at some length subsequently, in appropriate places. Others will be self-evident to the reader when, in later chapters, he encounters mention of the loss or gain of some feature by one group of animals or another.

Lampreys: The epidermis and dermis of the skin are never fused to the cornea to contribute respectively a corneal epithelium and a part of the substantia propria. A patch of visual cells is already functional in the primary optic vesicle (see Fig. 54c, p. 126) and persists as 'Retina

A' in the growing eye until metamorphosis, when throughout the remainder of the much-expanded retina ('Retina B') the visual cells are suddenly differentiated and the borders of Retina A become indistinguishable. Retina A goes out of function when the tiny larva first burrows into the mud, and the eye is blind until metamorphosis, when the skin covering it becomes transparent and Retina B matures. No intraocular muscles or suspensory-ligament fibers ever develop, for the pupil is motionless and there is no ciliary body interposed between chorioid and iris. The lens is propped in place only by the vitreous, which seems to have evolved its semi-solid nature for this original purpose.

Fishes: Except in the elasmobranchs, the optic vesicle is at first solid as is the central nervous system, both eye and brain becoming hollow secondarily. In many of the bony fishes the embryonic fissure never quite closes, and the chorioid erupts through it to form the 'falciform process'. Others develop, instead, a network of vessels at the vitreo-retinal interface. Those species which have a pseudobranch develop a huge capillary mass in the chorioid, the 'chorioid gland'. True lids and associated glands are usually lacking, though vertical, so-called 'adipose' lids are common.

Amphibians: The fusion of the skin with the purely mesodermal, inner layers of the cornea (those continuous with the sclera) is deferred until metamorphosis, as is the development of the lids. The growing suspensory-ligament fibers do not obliterate the anterior part of the secondary vitreous, but remain embedded in it so that no aqueous-filled cavities are ever formed behind the iris. Despite their entanglement, the tertiary vitreous fibers are derived only from the ciliary epithelium, the secondary vitreous solely from the sensory retina, just as in other vertebrates.

Reptiles and Birds: The neuroglial supporting tissue of the head of the optic nerve usually proliferates a vascular, pigmented 'pecten' projecting through the vitreous toward the lens. In birds the elongated base of the pecten follows the course of the embryonic fissure, developing from its lips. In some groups, an anterior portion of the embryonic fissure never closes, and a meridional slit is thus left in the ventral part of the ciliary body, through which the anterior and posterior chambers communicate. The third eyelid or nictitating membrane (present also, as the 'haw', in many mammals) arises as a vertical fold of conjunctiva at the nasal side of the eye, covered by the upper and lower lids. The equator of the lens and the ciliary body come into contact and remain

so (whereas in mammals they later separate, owing to the eye's growing faster than the lens, so that the suspensory ligament is thereby put in a state of tension, forcing the lens to become flatter during its growth). In the snakes, the course of development of many parts has been profoundly modified, as is explained in detail in section D of Chapter 16.

(B) Evolutionary

In its simplest terms as seen in the lamprey, the vertebrate eye has only a very few essential living parts: retina, uvea, fibrous tunic, and lens. The problem of the origin of the eye is merely the problem of the status of each of these parts previous to their present association. Yet though when thus stated the matter appears simple, it has baffled a great many astute morphologists. The great German anatomist Froriep once likened the 'sudden' appearance of the vertebrate eye in evolution to the birth of Athena, full-grown and fully-armed, from the brow of Zeus.

The Eye a 'Part of the Brain'—From the embryology of the eye it appears that there could have been no complex retina until the chordates had evolved an internal, tubular brain. The foveolæ opticæ have been interpreted as an ancestral stage in which the eyes were essentially a pair of photosensory epithelial pits in the skin, analogous to those of a modern *Nautilus*. Another possibility is that the foveolæ are developmental precocities without phylogenetic meaning. Before we can decide how to interpret them, we shall have to try to determine how far back the rods and cones may have been photosensory.

If the retina is thought of as a photosensory portion of the brain wall, outpocketed to keep it near the skin in an ancestor whose body was becoming larger and more opaque as evolution proceeded, then the sclerotic and uveal coats are easily disposed of by homologizing them with the meningeal envelopes of the central nervous system, the dura mater and the pia-arachnoid. The sclera is actually continuous with the dura via the sheath of the optic nerve. The latter also possesses a continuation of the pia-arachnoid, though this ends outside the eyeball and does not merge with the chorioid even in the embryo. The vascularity and pigmentation of the chorioid are however strongly pia-like characteristics, and in lampreys there are even striking histological similarities between chorioid and pia.

The big difficulties which an eye-origin theory must hurdle are: (*a*) the inversion of the retina—the fact that the vertebrate visual cells point away from the light; (*b*) the nature of the visual cells before they become photosensory, and the question of their location at the time they did so; and (*c*) the question of the status of the lens before it became associated with the retina as a dioptric structure.

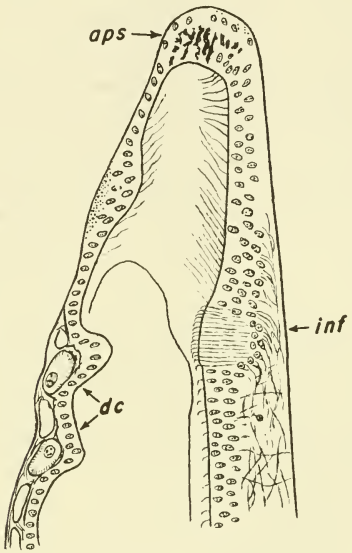

Fig. 45—Sagittal section of 'brain' of *Amphioxus*.

(In the position it normally has in the living animal in its burrow). From Walls, after Franz.

aps- anterior pigment spot; *dc*- two of the dorsal cells of Joseph; *inf*- infundibular organ, whose photosensory elements are flagellated ependymal cells.

Early Theories—Between 1874 and 1929 a series of investigators saw the beginnings of the vertebrate eye in the anterior pigment spot of *Amphioxus* (Fig. 45, *aps*). Even by 1890, however, experiments had indicated that this 'eye' is not sensory at all, and at the present time this is considered certain.

Lankester, in 1880, suggested that the eye of the vertebrate is comparable with that of the 'tadpole' larva of certain of the lower chordates, the Ascidia. Others interpreted this suggestion as one of true homology, and a debate sprang up over whether the ascidian eye was a degenerate

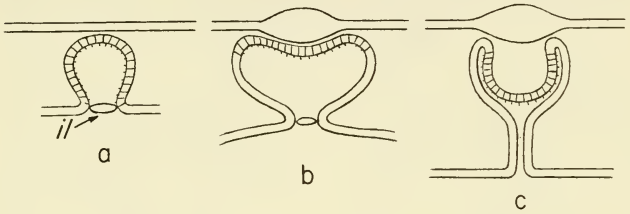

Fig. 46—Illustrating the ascidian theory as originally conceived.

(At a time when the ascidian lens was mistakenly believed to lie toward the brain cavity). From Walls, after Jelgersma.

a, ascidian eye, consisting of a retinal evagination of the brain wall and an internal lens, *il*.

b, hypothetical transitional stage in which two lenses were present, one on either side of the retina.

c, vertebrate retina and definitive, 'outer' lens, derived from skin.

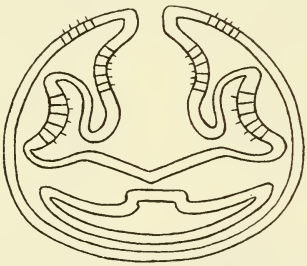

Fig. 47—Illustrating Balfour's theory. From Walls, after Parker.

Patches of photosensory cells are shown in the successive positions which they are supposed to have occupied before and after the evolution of the neural tube and the retinal evaginations thereof.

offshoot of the vertebrate organ or a primitive fore-runner thereof. Froriep later decided that neither of these views could be true, for the retina of the ascidian eye is not inverted; but he thought that both eyes might have had common ancestry in a pair of dermal eyes (Figs. 46 and 48).

Balfour's Theory—It was Balfour, in 1881, who first proposed that the vertebrate retina originated in the skin and was carried inside the animal by the evolution of the neural tube (Fig. 47). Several investigators, independently of each other, soon pointed out how well the fove-

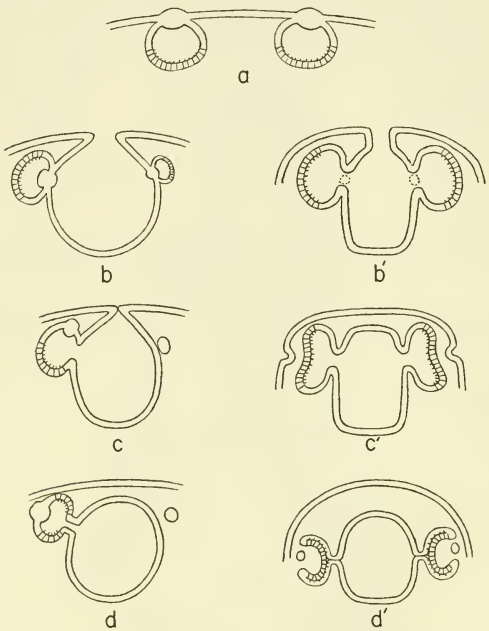

Fig. 48—Illustrating Froriep's derivation of the ascidian and vertebrate eyes. (From common-ancestral superficial vesicular eyes). After Walls.

a, b, c, d, stages in the evolution of the ascidian eyes, showing the degeneration of one member of the pair.

a, b′, c′, d′, stages in the evolution of the lateral eyes of vertebrates.

olæ opticæ fit into this hypothesis (Figs. 49 and 50). Balfour's theory was the first to account for the inversion of the retina, but it offered no explanation of the lens. It has however been suggested that inversion was no accident, but had to be brought about somehow if the highly meta-

bolic rods and cones were to have an adequate blood supply (the choroid) without this lying between them and the light and blurring the image. Moreover, it must be remembered that we have no certainty whatever that the chordate nervous system originated as a tube—the lowest vertebrates, which should show the most primitive situation, develop it as a solid cord and canalize it secondarily.

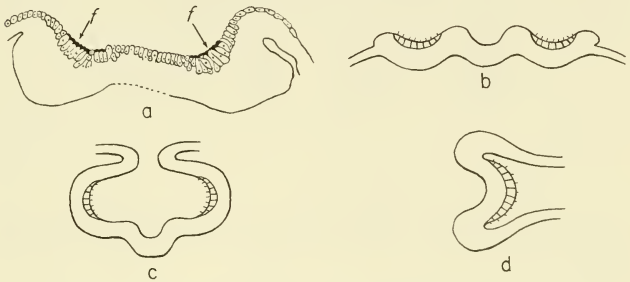

Fig. 49—The foveolæ opticæ in relation to Balfour's theory. From Walls.

a, unclosed brain region of neural tube of frog embryo, showing the foveolæ opticæ, *f-f*, as patches of pigmented columnar cells (after Franz).

b, c, d, stages in the evolution of the eyes, based on the development of the foveolæ into the retinæ (after Lange).

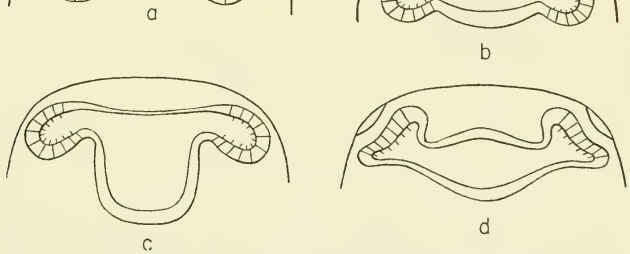

Fig. 50—Illustrating Schimkewitsch's version of Balfour's theory.

(Deriving the lateral eyes from one of several pairs of photosensory pits in the surface ectoderm, of which the foveolæ opticæ are the embryological counterparts). From Walls, after Schimkewitsch.

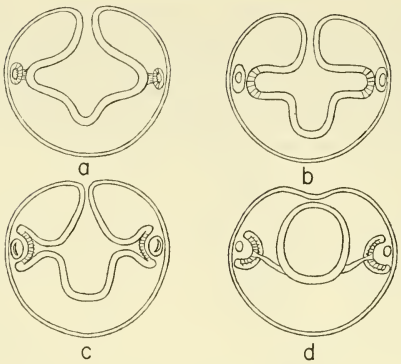

Fig. 51—Illustrating the placode theory. From Walls, after Béraneck.

A vesicular eye derived from a lateral-line organ loses its photosensitivity and becomes the definitive lens, while its ganglion becomes photosensory and is converted into the definitive retina.

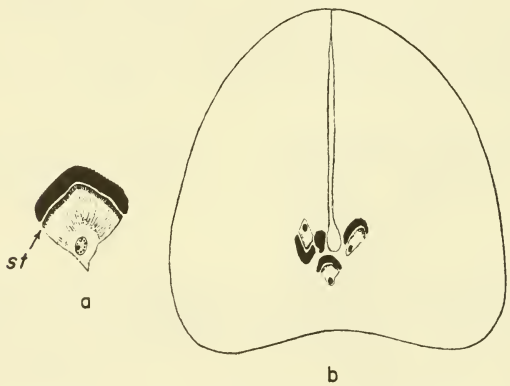

Fig. 52—Hesse's organs of the 'spinal cord' of *Amphioxus*. From Walls, after Hesse.

a, a single organ, consisting of a pigment cell and a photosensory ganglion cell, whose 'stiftchensaum', *st*, was believed by Boveri to be a cuticular structure comparable with the outer segment of a rod or cone.

b, cross section of nerve cord, showing various orientation of the organs (enabling the animal to respond to the direction of light).

The Placode Theory—The origin of the lens was first explained by Sharp in 1885. He regarded the lens as a modified lateral-line organ which was, like those organs, a sensory ectodermal pit or bud. The 'placode theory', an extension of Sharp's original idea, proposes that the lens was once the whole eye and that the present retina served as its ganglion, eventually taking over the sensory function itself and releasing the vesicular 'skin' eye to become a lens (Fig. 51). Fatal objections to this interpretation of the retina arise from the utter absence of embry-

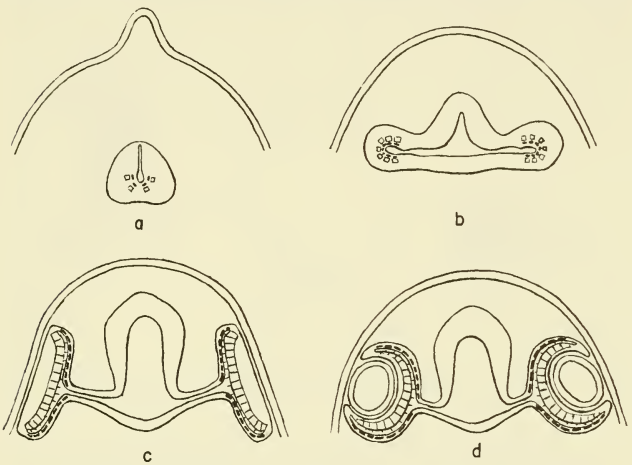

Fig. 53—Illustrating Boveri's theory. From Walls, after Boveri.
The Hesse's organs become the visual and pigment-epithelial cells of the vertebrate retina.

ological confirmation of any previous connection of retina and lens, and from the lack of any evidence that a self-determining lens placode exists at all as a morphological entity—it will be recalled that it is called into existence ontogenetically solely by the chemical influence of the optic cup. Nor does the placode theory account for inversion.

Boveri's Theory—Inversion was explained anew by Boveri in 1904, in a theory that made use of the two-celled visual organs of *Amphioxus*, which had been discovered by Hesse in the 'spinal cord' of this so-called grandfather of the vertebrates (Figs. 52 and 53). While Boveri's theory

offers no account of the lens, it gives as good an explanation of the retina and its inversion as does Balfour's theory; and both hypotheses are widely taught at the present time. Acceptance of either is impossible, however, unless the mode of development of the rods and cones indicates either that they might have been already photosensory while still in the skin,

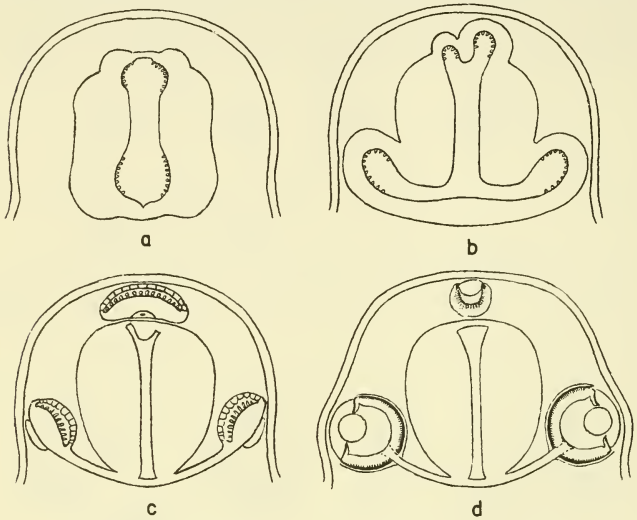

Fig. 54—Illustrating Studnička's theory. From Walls, after Studnička.

The sensory cells of the median and lateral vertebrate eyes are derived from the flagellated ependymal cells which line the neural tube. c represents the larval lamprey, in which the eye is temporarily functional though the retina ('Retina A'—see p. 117) is still only an uninvaginated optic vesicle and the lens is flat and useless.

or that they might have been derived from the photosensory ganglion cells of Hesse's organs or the similar 'Joseph's cells' in the head region of *Amphioxus* (Fig. 45, *dc*).

Studnička's Theory—Unfortunately the cytogenesis of the rods and cones supports neither Balfour nor Boveri, but confirms a radically different hypothesis first offered in 1912 by Studnička, and which has yet to be given consideration in any of the various text-books which afford a little space to the eye-origin problem (Fig. 54).

Studnička noticed that if one traces the visual-cell side of the inner layer of the optic cup around the latter and through the optic stalk into the central nervous system, one emerges into the ependymal layer of the brain wall. The ependymal cells lining the cavities of the brain and cord are non-nervous supporting elements which often bear flagella (microscopic whiplashes) which circulate the cerebrospinal fluid. Studnička also laid great stress upon the eye of the young larval lamprey (Fig. 54c), which is precociously functional while still merely an optic vesicle, as indicating that the vertebrate eye was originally merely a 'directional'

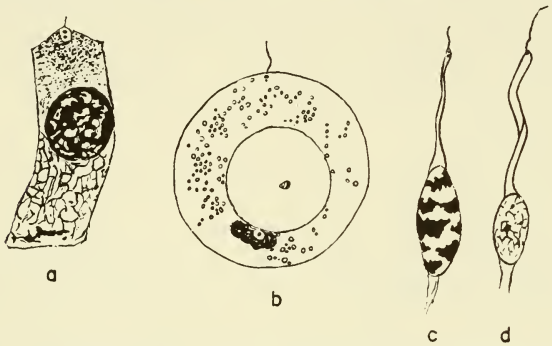

Fig. 55—Comparability of young visual cells with ependymal and other flagellated cells: embryological support for Studnička's theory. From Walls.

a, fetal human foveal cone, showing filamentous, centrosomic anlage of outer segment rooted in diplosome (after Seefelder). b, immature human sperm cell showing anlage of flagellum, consisting of centrosomic filament and diplosome (after Gatenby and Beams). c, immature cone from retina of kitten (after Leboucq). d, ependymal cell from brain of carp (after Franz).

one before it became capable of forming images. Since the lens is already present in the tiny lamprey, but in the form of a flat cushion incapable of dioptric function, Studnička argued that it must have existed phylogenetically—a vestigial remnant of something else, possibly a sense-organ—before the retina was devised at all. He also showed that there are many central-nervous sense-organs in vertebrates, including the median or pineal and parietal eyes (see Chapter 10, section D), whose receptors are certainly modified ependymal cells. He has received striking confirmation in the recent demonstrations of the photosensitivity of the lining of the diencephalon of many forms, which (in birds) has been

shown by Benoit and others to act as a photic receptor organ, controlling reflexly the annual spermatogenetic cycle.

But Studnička never considered in detail the manner in which rods and cones differentiate, though this had already been most carefully worked out by several European investigators. If he had done so, his theory would surely have seemed much stronger to subsequent text-writers. For the outer segment, the receptive organelle, of a vertebrate visual cell develops exactly like any flagellum (Fig. 55a, b). It starts as a filament of centrosomic material rooted in a diplosome or dumb-bell shaped centriole embedded in the future inner segment, later becoming encrusted and thickened by mitochondria which form the conspicuous spiral filaments making up the bulk of the outer segment (Figs. 23a, 25c, pp. 55, 62; Fig. 26b, B, p. 63). A closer comparability of visual cells and ependymal cells (Fig. 55c, d) could hardly exist.

Origin of the Retina—If the photosensory parts of the rods and cones were once ependymal flagella, it is certain that Boveri's theory must be discarded; for ependyma, even photosensory ependyma, exists in *Amphioxus* side by side with the Hesse's organs and Joseph's cells. It is equally certain that the vertebrate retina could not have gotten started, as a photosensitive region of the brain wall, until the latter had become tubular. Only then was there any need for the ependymal cells to evolve as elements distinct from nerve cells; and these were primarily supportive (they still run through the whole thickness of the brain wall in *Amphioxus* and the lampreys), then secretory in function (producing the cerebrospinal fluid) before it became necessary for them to aid in circulation by means of flagella. No flagella, no sensitivity or photosensitivity; and it can be regarded as certain that the definitive visual cells were developed within the finished brain and not, à la Balfour, while the nervous system was still a part of the skin. Indubitably there were photo-irritable cells in the provertebrate's skin, as there still are in many fishes and amphibians—even in cave forms which are never normally struck by light; but these lost importance as soon as photosensory ependyma had appeared (Fig. 56). The most primitive homologues of the rods and cones to which we can point today are the photosensory flagellated ependymal cells of the 'infundibular organ' of *Amphioxus* (Fig. 45, *inf*, p. 120), which is a crude visual apparatus seemingly for the detection of the direction of light by means of shadows cast upon it by the anterior pigment spot.

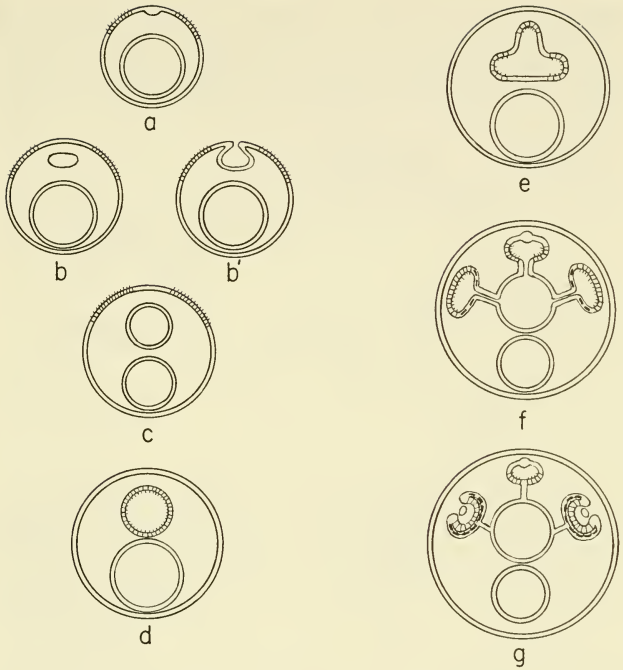

Fig. 56—Origin of the retinæ of the median and lateral eyes. After Walls.

a, pro-vertebrate stage with photosensory ectoderm and with the nerve cord still a part of the skin. b, b', alternative stages in the evolution of the neural tube, depending upon whether one adheres to the 'solid' or 'hollow' doctrine. c, tubular nervous system formed, but with ependymal lining purely sustentative, secretory, and circulatory. d, ependyma has become photosensory locally, and photosensory cells have disappeared from the skin. e, f, g, stages in the evolution of patches of photosensory ependyma into retinæ.

Origin of the Lens—When everything else in the primitive eye is so plausibly explicable, it is really a shame that we cannot be at all sure how the lens came into existence. The lens placode fits neatly into the set of cephalic lateral-line organs, and for it to develop into a lens is no more remarkable than for one of them to generate the olfactory organ or for another of them, the otic placode, to differentiate into the elaborate

membranous labyrinth of the internal ear. It would be nice to be able to insist that the lens placode has a real morphological existence and that the lens is therefore a captured lateral-line organ, as Sharp believed; but we cannot do so with clear consciences. The best that can

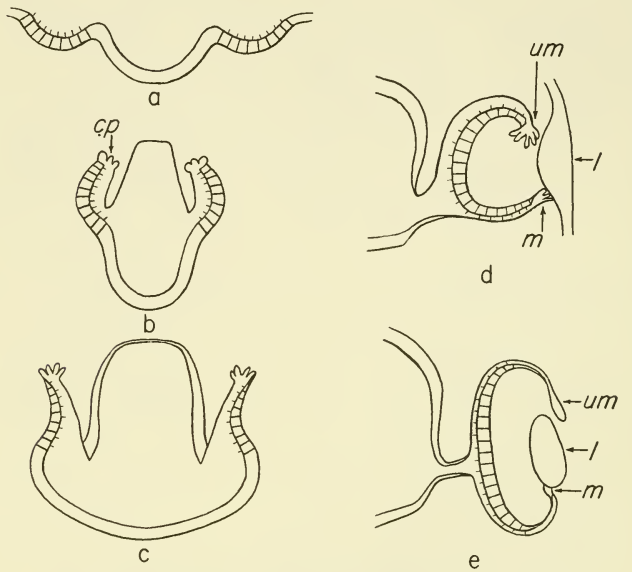

Fig. 57—Illustrating Tretjakoff's theory. From Walls, after Tretjakoff.

a, foveolæ opticæ stage. b, stage of closed neural tube, showing hypothetical chorioid plexus, *cp*. c, hypothetical stage in which the expansion of the chorioid plexus has created the pigment epithelium and, by forcing the sensory retina to curve, is producing a two-layered cup. d, stage in which the attachment of the cup to the skin is evoking a muscle, *m*, and a lens, *l;* a remnant of the chorioid plexus forms the umbraculum, *um*, corresponding to the pupillary nodule of an amphibian. e, final condition of fish eye with free lens, *l*, operated by retractor lentis muscle, *lm;* from the umbracular remnant *um* a lens may be regenerated, as in salamanders (*cf.* Fig 106a, *pn*, p. 266).

be said is that *perhaps* a former self-determination of the lens has been replaced by a more convenient immediate chemical control by the optic vesicle—just as the development of a secondary sexual character may be under genetic control in one species of bird, while in another the

same character is caused to develop by hormones, and fails to appear if the gland which secretes the chemical determinants is removed.

No other current explanation of the lens is anything but lame. The co-existence of a functional retina and a functionless lens in the larval lamprey may mean, as Studnička thought, that the lens existed in some other status before the rest of the present eye evolved. Possibly however it means no more than does the precocious presence of functionless muscles in an embryo before their nerves have grown out to connect with them. No one would argue that this means that those muscles once functioned without nervous control.

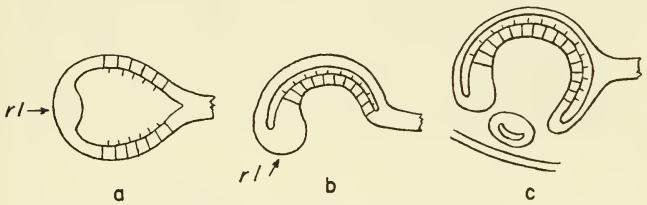

Fig. 58—Illustrating Schimkewitsch's theory. From Walls, after Schimkewitsch.

a, hypothetical ancestral skin-eye, with erect retina and intrinsic 'retinal' lens *rl*. b, phylogenetic stage comparable with embryonic cup—the eye, originally dorsal, has swung laterally and ventrad, becoming passively indented (by resistant tissue) to create the embryonic fissure; the retinal lens is now uselessly located. c, final condition of the eye, with new lens derived from the skin; it is from the site of the supposed original retinal lens that new lenses may be regenerated if the skin-lens is removed in the young embryo or even (salamanders) in the adult.

Tretjakoff thought that the primitive optic cup was attached to the skin and developed contractile elements there (which later became the piscine retractor lentis muscle) for producing to-and-fro accommodatory movements of the optic cup relative to the skin. The lens then arose as a sort of callus in response to the continual pull of the muscle cells (Fig. 57). But the lower fishes have no retractor lentis; and in any case there would have been no need whatever of accommodation until the lens had already appeared and become capable of forming a crisp image. Tretjakoff also attempted to account for the fact that in salamanders whose lenses are removed, new lenses may regenerate from the dorsal pupil margins. This has been explained more cleverly, if no more properly, by Schimkewitsch (Fig. 58).

Franz's theory is new and ingenious. He suggests that the lens evolved, when the neural tube was just closing, in such a position as

to concentrate light upon the photosensitive lining of the diencephalon. Its locus somehow escaped involution with the neural tube and later moved laterally to be taken over by the new retina (Fig. 59). No ontogenetic conditions support this idea, and like the placode theory it stands or falls with the demonstrability of a self-differentiating lens anlage.

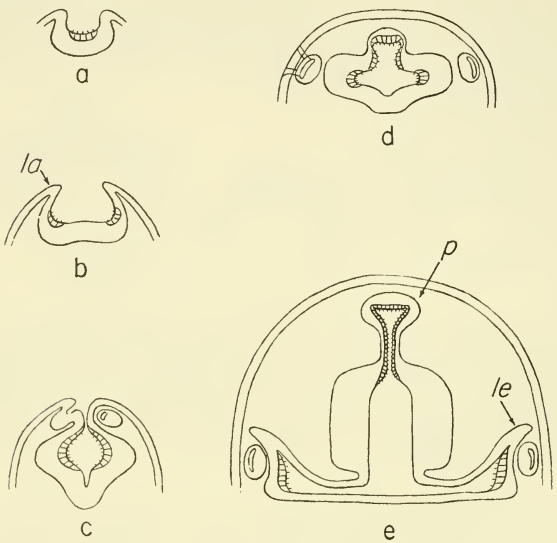

Fig. 59—Illustrating Franz's theory. From Walls, after Franz.

a, ancestral surface eye corresponding to the infundibular organ of *Amphioxus* prior to the closure of the neural tube. b, later stage corresponding to the foveolæ opticæ, with the future lens-forming area labelled *la*. c, stage of general photosensitivity of lining of diencephalon. The lens (shown in an earlier stage on the left, a later one on the right) is evolving just outside the region of involution. d, stage of appearance of dorsal diencephalic evagination—the future pineal eye; the lentogenic areas have shifted still farther laterally. e, final condition of the pineal (*p*) and lateral eyes (*le*); the lens is now embryologically derived from the skin far distant from its original location.

The experimental morphologists are very fond indeed of doing things to embryonic eyes to see what they will do in return. Someday, their juggleries may disclose that in some species of fish or amphibian a lens will start to develop without the presence of an optic vesicle. Until

then at least, and perhaps forever, the evolutionary origin of the vertebrate lens must remain a tantalizing mystery.

A very good question is: how is it that the lens, derived from the skin, lies inside the fibrous and uveal tunics—which, above, we homologized with the meningeal coats of the brain? Did the retina acquire its optical partner before the central nervous system acquired its protective sheaths? Perhaps so—and, such theories as that of Tretjakoff make such an assumption necessary. But the lens could easily enough have gotten through the sclerotic coat after the latter had evolved. Such legerdemain is common enough in vertebrate history—as witness the presence of the pectoral girdle *inside* the rib basket, in the turtles. All that is needed is a nice timing of embryological events, occurring as an embryonic mutation—if the lens did pass through the dura mater to get inside the eyeball, it assuredly did so in one jump, in some ancient embryo in which the condensation of the dura happened to be delayed. And lenses have been getting inside of eyes *ontogenetically* in that same way ever since.

Chapter 6

ELEMENTS OF VERTEBRATE PHYLOGENY

If one knows something of the history of a group of animals and its position in the animal kingdom, one may more easily draw correct conclusions as to how it acquired its characteristic morphology. We may learn of some structure in the eye of one of the lower animals which looks intriguing as a possible forerunner of some detail of the human eye; but we need to know whether the group that exhibits the structure in question is anywhere near the main line of evolution, or represents a blind alley from which nothing higher than itself has ever emerged.

A little about vertebrate group inter-relationships is therefore included here, that the reader may better understand why one animal has solved a given visual problem in one way while another, given other raw materials, has had to find a different—perhaps better, perhaps poorer—solution to the very same problem. In devising adaptive structures, each animal group has had to do what it could with the materials at hand—the assemblage of characteristics and structures with which the group happened to be endowed when it crystallized out of the stream of life. May we reasonably look to the teleost fish for the prototype of some amphibian ocular structure? Can we expect to see in the snakes a feature which the lizards discarded? Can we fairly compare the human eye more closely with the eye of a salamander, or with that of a bird? A brief review of the vertebrate pageant will help the reader to answer such questions as they arise during his study of subsequent chapters.

At the bottom of the vertebrate scale stand the cyclostomes; and just above them, the many types of true fishes. From one of these types the first land animals, the ancient amphibians, were derived. They in turn gave rise on the one hand to the modern amphibians and on the other to the reptiles. The reptiles differentiated into a large number of orders, only four of which have persisted to the present day. From one group of extinct reptiles came the birds; and from another (much older) group, the mammals—warm-bloodedness and heat-retaining coverings (feathers, fur) thus having originated independently in the two highest classes of vertebrates.

The lowest of the vertebrates are the cyclostomes, so named for their round, suctorial, jawless mouths. The cyclostomes include the hags, whose eyes are microscopic and functionless, and the lampreys (Fig. 60). They are eel-shaped, blood-sucking parasites upon fishes. Some small

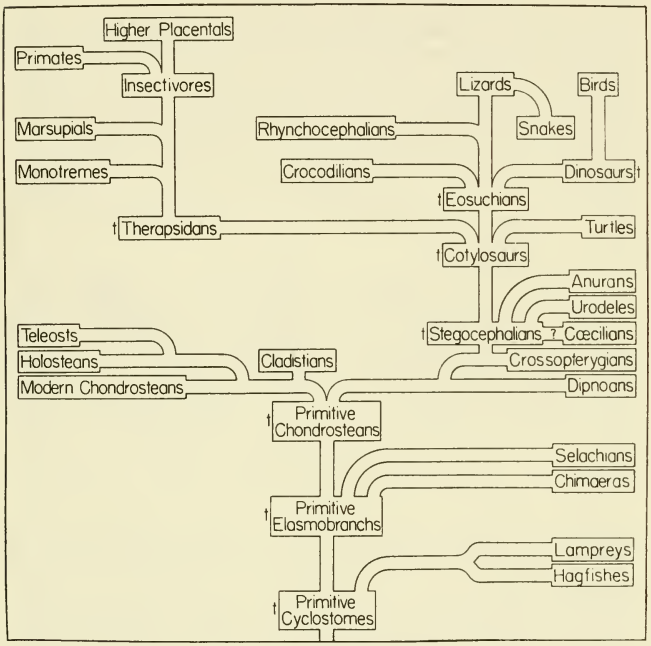

Fig. 60—Inter-relations of the major groups of vertebrates.
Only those extinct groups (marked †) are shown which actually link up living assemblages.

freshwater lampreys have given up parasitism and do all of their feeding as larvæ, breeding for the first and only time a few months after transforming to the adult condition. Parasitic lampreys also breed but once after years of vegetative activity, and then die. Cyclostomes have no scales or paired fins, and many other things about their anatomy are

simple; but it is sometimes difficult to know whether to attribute the simplicities to primitiveness or to the secondary simplification (mistakenly called degeneracy) which is a part of their adaptation to a parasitic mode of life. As regards the lamprey eye, however, there is unanimous agreement among modern students that its features are all primitive and show no indications of degeneracy.

The oldest of the true fishes are the elasmobranchs, whose modern representatives, the Selachii (sharks and rays) and Holocephali (chimæras), are very different from their extinct progenitors. The elasmobranchs were derived from ancient cyclostomes, but not from lamprey-like ones. Like the cyclostomes, they have cartilaginous skeletons; but they also have paired fins, jaws, and scales. From those jaws have come the little bones of the ossicular chain which traverses our middle-ear cavity; and from some of the rows of scales on the elasmobranchs' lips came their teeth, the ancestors of our own—and very different from the horny teeth of lampreys.

The primitive elasmobranchs were a main-line group, for from them have come all of the higher, 'teleostome' fishes; and through these, the terrestrial vertebrates. From ancient elasmobranchs there arose an advanced group of fishes, still with cartilaginous skeletons, called the Chondrostei. These fishes have had many descendant groups, among them several which might, any one of them, have given rise to land forms—for they all spread into fresh waters and swamps, and developed lungs of sorts, and limb-like fins with which to drag their bodies over the slime.

These lunged fishes were the Cladistia, the Crossopterygii, and an offshoot of the latter called the Dipneusti—the lung-fishes proper. All three of these groups were once numerous as to species and individuals, but have dwindled to remnants which still cling precariously to life in competition with the more advanced modern fishes. The Dipneusti, or dipnoans, have but three living genera: *Neoceratodus* in Australia (Fig. 61a), the African *Protopterus,* and *Lepidosiren* in South America. There are but two living cladistian genera—*Polypterus* and *Calamoichthys,* both in Africa. Until very recently it was supposed that the crossopterygians were extinct; but one species, named *Latimeria chalumnæ,* was lately discovered in the sea off South Africa. This is the only archaic teleostome known from salt water.

The chondrosteans have persisted to the present time, but are now represented only by the sturgeons (*Acipenser, Huso, Scaphirhynchus,*

etc.) and the spoonbills or paddlefishes, *Polyodon* and *Psephurus*. Very soon after their own origin, the chondrosteans gave rise to a group of fishes with bony skeletons, the Holostei—formerly lumped with the Chondrostei in an artificial group called the 'ganoids'. The Holostei had their heyday long ago, and have but two living genera, the bowfin (*Amia*) and the gars or gar-pikes, *Lepisosteus* spp. From primitive holosteans came the Teleostei, the most conspicuous group of modern fishes, including such familiar forms as the trout, perch, herring, and goldfish. Defeating the holosteans in competition for habitats and food, the teleosts have taken the place in the seas and fresh waters formerly occupied in succession by the chondrosteans and holosteans. But the teleosts are a blind-alley group from which no higher forms have been derived.

Fig. 61—The transition from water to land.

a, an existing dipnoan, the Australian 'dyelleh', *Neoceratodus forsteri*. After Ley.

b, a giant stegocephalian, *Mastodonsaurus giganteus* (redrawn by E. C. Case, from a restoration by Fraas); in life, the animal was about fifteen feet long. *p*- site of pineal eye.

It was probably from swamp-dwelling crossopterygians that the first land vertebrates came. These were the extinct amphibians which we call the Stegocephali, from their characteristic head-armor. Some adult stegocephalians were but a couple of inches long, but most of them were gross, sluggish beasts of little brain (Fig. 61b)—very different from the pert little salamanders and agile frogs of the present time. It is possible that the Stegocephali are not a natural group, but comprise two groups with independent origins. It is also barely possible that some of the modern amphibians originated directly from air-breathing fishes and not from the Stegocephali. These questions have only recently been raised and are not yet settled. At any rate, it is certain that the Stegocephali were

the immediate ancestors of the reptiles—which, with their dry, scaly skins and a number of internal improvements, were the first vertebrates to become quite divorced from the waters.

The first land vertebrates must have had an easy time of it. Escaping the fierce competition of the waters, they found themselves exploring a new world in which they had no enemies. There was abundance of food, for the plants had taken to the land eons before. The very ease with which the land animals could spread and multiply encouraged the rapid production of new types. And then, the inevitable happened—some of these newer forms found the older ones good to eat. Competition on land eventually became so keen that many reptiles, mammals, and even birds returned to an aquatic existence. On land, their muscles had had to sustain their weight and had become far more powerful than those of fishes. Claws, beaks, and crushing teeth had also evolved, and with such superior weapons many species found it easy to get a living in the water.

The reptilian group flourished amazingly and ruled the world for tens of millions of years through its aristocracy, the group we call the dinosaurs. But even while the twenty-foot tyrannosauri were mangling the ninety-foot diplodoci, the first of the mammals were furtively sneaking about looking for dinosaur eggs to suck, and the first birds—derived from tiny dinosaurs—were getting off the ground for short flights. The reptiles which we have around us are a mixture of old and new. The lizard-like *Sphenodon* (rapidly approaching extinction on a couple of New Zealand islands) is the sole survivor of the rhynchocephalians, the rest of which died with the dinosaurs. The turtles are of enormous antiquity—turtles are among the oldest reptilian fossils we know of, and they were already perfectly standard turtles "way back then'. The ancestors of the crocodile group can also be traced back into the beginnings of the Age of Reptiles.

The lizards, however, came into existence only recently as an offshoot of the extinct mosasaurs. The snakes originated as legless lizards, so very recently (as geological time intervals go) that the most primitive of them, the boas and pythons, still have vestiges of the hind legs. Legglessness has since arisen independently several times in different families of existing lizards, but these snake-like forms are still true lizards.

The mammals fall into three great divisions: the egg-laying monotremes of which only the duck-billed platypus (*Ornithorhynchus*) and the echidnas are left on earth; the marsupials, which originated in South America and left primitive types there, but reached their culmination

in Australia where they had no competition from the higher mammals; and the placentals, which are the familiar hairy, milk-secreting animals of the world and the group to which man himself belongs.

As one would expect, the birds, the monotremes, and even the marsupials have quite a bit in common anatomically with the reptiles. But the placental mammals are quite distinct—more different from the monotremes than the latter are from the reptiles. This is especially true as regards the eye; and from ocular and other considerations Franz has postulated that the placental mammals originated, not from lower mammals, or (Huxley's view) independently from reptiles, but from forms intermediate between the amphibians and the reptiles. There is however no palæontological justification for such a view. The reptiles and birds are so closely related that they are commonly lumped together as the 'Sauropsida'; and monotreme eyes—to some extent also marsupial eyes —are sauropsidan in plan except for a radical simplification of the mechanism of accommodation. The eye of the placental mammal is more like that of an amphibian than like that of a reptile, but this is no proof that the placental mammals originated more or less directly from amphibians. A more likely view is that the placental mammals had an early history of strict nocturnality, during which they depended largely upon other senses and simplified the eye far below the level of complexity of the eye of the reptilian ancestor. The placental eye thus came to simulate the amphibian eye through what might be described as a reversal of evolution.

For our purposes the placental mammals may be roughly divided into 'lower' and 'higher' orders—the former including the insectivores, primates (including man), bats, sloths, armadillos, ant-eaters, and the 'flying lemurs' (*Galeopithecus* and *Galeopterus*); and the latter comprising the carnivores, seals, whales, and hoofed animals (including the elephants, hippos, etc.). The rodents and lagomorphs may be assigned to the top of the lower series or to the bottom of the higher, depending on one's point of view.

The tree-shrew and the aye-aye are thus at the bottom of the group and the elk and tiger are at the top—with man very close to the bottom biologically, ranking high only psychologically, as regards his brain and mind. Man's order, the Primates, split away from the Insectivora about 50,000,000 years ago. Most of the living groups of mammals have come into existence since that time. Man himself came along only yesterday, but his *stock* is older than most of the mammalian stocks around him.

Part II – Ecologic

Chapter 7

ADAPTATIONS TO ARHYTHMIC ACTIVITY

(A) The Twenty-Four-Hour Habit and the Eye

Of the ways in which natural light can vary, it is the variation of its intensity which is of most importance to animals, and to which they have responded by the most profound of ocular modifications. To adopt the bright hours of day, or the dim ones of night, or to appear indifferent to their alternations, all require adaptations of the eye. These adaptations for high sensitivity or for relative insensitivity in turn make possible, or tend to forbid, concomitant adaptations for form-perception and visual recognition on a basis of pattern and color. Animals have had to balance the desirability of a given habit with their ability to use the advantages, and tolerate the disadvantages, which the modifiability of their eyes in the appropriate direction confers or limits. In this and the two succeeding chapters we shall examine the adaptations to illumination-preferences which vertebrate eyes have produced.

In surveying the visual habits of vertebrates one's attention is naturally caught by the extreme conditions of strict diurnality and strict nocturnality, and one tends to suppose that the intermediate condition or arhythmicity, of apparent indifference to night and day, represents a failure to specialize and a lack of adaptation. This is never actually the case—a truly unspecialized and intermediate type of eye would fit its possessor, not for twenty-four-hour vision, but for only the brief periods of morning and evening twilight. The arhythmic animal has to meet a more severe set of requirements than does the rhythmic one of either extreme type, and meets them by *combining* in one visual organ those adaptations to both bright and dim light which are not mutually exclusive. To anticipate the next two chapters, a strongly yellow lens (as in the prairie-dog) goes with diurnality but makes vision in dim light impossible; and a tapetum lucidum facilitates nocturnality but if non-occlusible and associated with a super-sensitive retina unprotected by a slit pupil (as in the opossum), it demands that the animal scrupulously avoid strong light. Obviously, any attempt by an animal to secure twenty-four-hour vision by combining a yellow lens with a tapetum would result in his having wretched vision at any and all times.

In either type of rhythmic animal we may have fancy adaptations, yet an ocular situation which is simple in that it is static. But, for an animal to become capable of arhythmic, twenty-four-hour activity, it is incumbent upon him to evolve a more flexible set of ocular features, capable of physiological change to embrace a wide range of stimuli—in other words, a dynamic eye in which, when the animal passes from one extreme of illumination into the other, something or several things can be seen to happen, and can be seen to be adjustive. The photomechanical changes of the iris and the retina are the most conspicuous 'somethings' referred to. Adaptation to twenty-four-hour vision has its static end-products as well, in the evolutionary alteration of the cone:rod ratios of a rhythmic ancestor, or even in the production of a duplex retina from an ancestrally simplex one by the transmutation of cones into rods or vice versa.

Before we take up these physiological and phylogenetic methods of adaptation toward all-round visual capacity, it will be well to have certain ecological definitions well in hand. We find that animals may be classified as:

A. Diurnal; by which we shall take to mean that they are active chiefly in the daytime, occasionally also in bright moonlight. Such animals have eyes which are incapable of dim-light vision.

B. Crepuscular; that is, active only in either or both of the evening and morning twilight periods. Requires more sensitive eyes, which are truly neutral, with few or no adaptations for extremes of illumination.

C. Twenty-four-hour—more properly, 'arhythmic', the former term applying better to both eye and animal, and both terms signifying that the animal is about equally active by night and day. Such animals, if they sleep at all, do so by irregular cat-naps.

D. Nocturnal; being active chiefly at night and confining daytime activities largely to passive basking. Eyes usually more sensitive than those of twenty-four-hour animals, and with much better devices for greatly reducing sensitivity in daylight.

E. Strictly Nocturnal; with such sensitive eyes, so lacking in sensitivity-reducing devices, that the animal is secretive or quiescent by day.

Each of these categories blends and intergrades with the next. Particularly is this true between *'C'* and *'D'*, in which groups fall nearly all of the mammals with the larger ones leaning toward *'C'* and the smaller species inclining strongly toward *'D'* or *'E'*. The chief assemblages of

class 'C', twenty-four-hour vertebrates, and their principal bases for all-round visual capacity, are:

The teleost fishes, relatively few of which are *strictly* diurnal, nocturnal, or crepuscular. Their ability to regulate ocular sensitivity resides almost wholly in their rod-rich retinæ, in the form of efficient photomechanical changes. Very few have mobile pupils.

The frogs, which again rely chiefly upon retinal adjustments and possess at least one diurnal adaptation (yellow oil-droplets) which the toads and the salamanders have had to eliminate, in order to become respectively nocturnal and secretive.

Many slit-pupilled reptiles, which, being poikilothermous, tend to bask in the sunshine rather more than would a warm-blooded animal with the same general type of eye. The crocodiles and particularly the geckoes have such excellent pupillary control of sensitivity that they are practically arhythmic though tending to feed more at night.

The larger terrestrial mammals—ungulates, elephants, and large carnivores such as the wolves, bears, lion, etc. Here alone do we find twenty-four-hour eyes which physiologically are relatively static, with neither special retinal nor, as a rule, extensive pupillary regulation of sensitivity. These forms straddle the fence by having enough rods-per-cone to secure fair intrinsic retinal sensitivity, with large eyes and large retinal images to obtain good resolution of details despite the paucity of cones. They compensate for the lowered illumination of the larger image by placing behind the retina a sensitizing device, the tapetum, which is elsewhere found chiefly among the best-adapted of nocturnal vertebrates. The vision of these mammals both by night and by day is good enough so that they *depend* on it. Hearing and scent are important enough at long range, but the serious business of stalking involves vision, whatever the illumination. Day or night, a sightless carnivore would be helpless—and so would a blinded ungulate.

(B) Retinal Photomechanical Changes

The phenomena which are grouped under this heading were discovered one by one in the 1877-1887 decade. They consist of changes of position, in bright and dim light or darkness, of the retinal pigment and the visual cells, and of minor changes in shape and position of some of the retinal nuclei. The nuclear changes are largely passive and are of no known significance for vision; but the migrations of the rods, cones, and retinal pigment are of great importance in the lower vertebrates.

Pigment Migration—It will be recalled that the cells of the retinal pigment epithelium often bear groups of long processes which interdigitate with the visual cells (Fig. 20d and e, p. 44) and that in the latter a portion of the inner segment between nucleus and ellipsoid is often contractile and then bears the name of myoid (Figs. 22, 23, 24; pp. 54, 55, 59). It is the retinal pigment (fuscin) in the pigment-cell processes, and the rod and cone myoids which are chiefly concerned in the photomechanical changes of the retina. These changes are most conspicuous in duplex retinæ and are concerned with both light- and dark-adaptation of the retina.

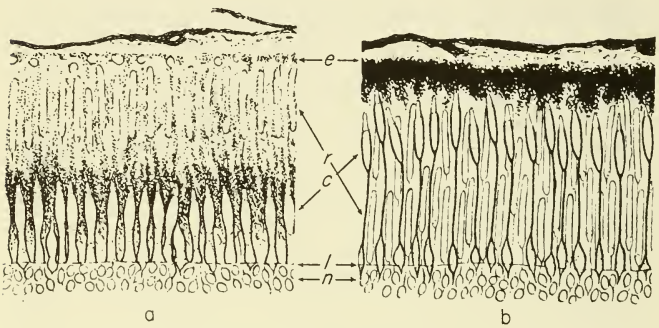

Fig. 62—Photomechanical changes in the retina of a fish, *Phoxinus lævis*. From Kühn, after von Frisch.

a, visual-cell layer and pigment epithelium in light-adaptation. b, dark-adaptation. *e*- pigment epithelium; *r*- rods; c- cones; *l*- limitans; *n*- nuclei of visual cells.

When an animal equipped with photomechanical changes emerges into bright light, a large portion of the retinal pigment—that which is in the form of rodlets or short needles rather than tiny spherules—starts to flow slowly down into the pigment-cell processes. These may be numerous and so slender that the granules pass into them in single file, or they may be fewer and much more bulky. In as little time as half an hour (though usually more slowly) the pigment will be found to be largely scattered along the length of the processes and may reach nearly to the external limiting membrane, being piled up into a dense mass at this limit of its excursion. It thus forms a system of cylindrical sheaths sur-

rounding the visual cells and blocking off from them any light rays which approach them at angles to their axes. Where the myoids are very slender (as in most fish rods) the expanded pigment may close in densely enough between the rod ellipsoids and the limitans to shut off even the axial rays from the percipient outer segments of the rods (Fig. 62).

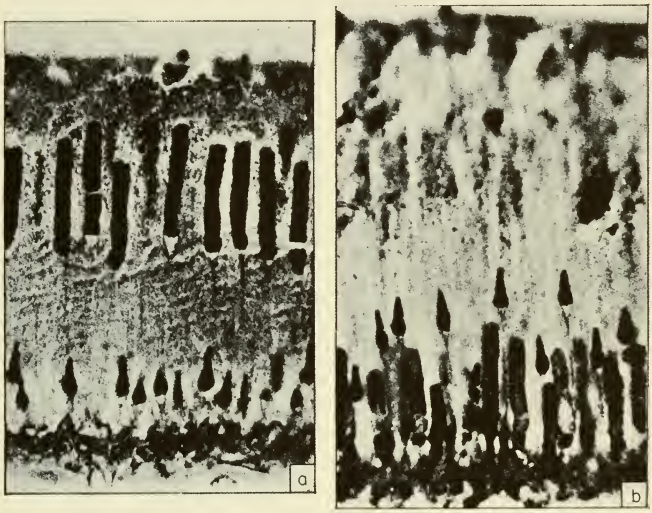

Fig. 63—Visual-cell migrations in a catfish, *Ameiurus nebulosus*. × 500. After Welsh and Osborn.

a, depigmented section of light-adapted retina, showing rods elongated toward pigment epithelium and cones retracted toward external limiting membrane.

b, depigmented section of dark-adapted retina; cones elongated, rods retracted.

Visual-Cell Movements—Cones always escape being thus shielded to any extent by the expanded, light-adapted pigment. They either sit, permanently, directly upon the limitans or, if migratory, contract into that position—away from the advancing pigment—in the light. Rods however, if they migrate at all in bright light, do so in the direction toward the pigment (Figs. 62 and 63). The effective covering of the rods by pigment is thus the sum of the pigment expansion and the elongation of

the rod myoid. The two movements are not perfectly synchronized, however, for the visual cells usually complete their migrations much more rapidly than does the retinal pigment, though always consuming from several minutes to an hour or more in the process, in different species. There may be both indefinite and very definite differences within a single

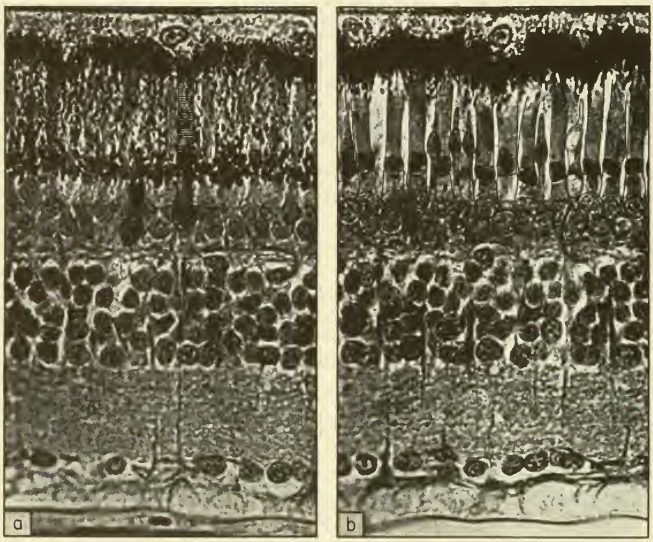

Fig. 64—Photomechanical changes of the leopard frog, *Rana pipiens*. × 500.

a, ventral periphery of light-adapted retina. The expanded pigment obscures the visual cells, but a cone and a rod have been emphasized to show their positions.

b, same region, dark-adapted. The outlines of the visual cells have been reinforced. Note that the cone myoids are greatly lengthened, the rod myoids somewhat shortened, as compared with a. Toward the right is a double cone, whose chief member has migrated but whose accessory member never leaves the limitans (*cf.* Figs. 22c, 23d, 24b, pp. 54-59).

retina, for the cones may be either uniform or very ragged in their responses, and both pigment and cones may respond less in particular retinal areas than in others. In fishes the single and twin cones migrate at different rates to different extents, and in other vertebrates the accessory members of double cones never migrate whether the chief cones do or not (see Fig. 24, p. 59, and Fig. 64b).

If the animal now enters darkness or even a dimly-lighted situation, the movements proceed, more slowly than in light-adaptation, to reverse themselves: the pigment granules glide back up out of the processes and concentrate as a dense band in the cuboidal cell-bodies of the epithelium, the rod myoids shorten and draw the sensitive outer segments away from the pigment and thus toward the light, and the cone myoids elongate to push the cone bodies toward the pigment—sometimes to no apparent purpose, but in some animals thereby making appreciably more room for the rods to gather in a smooth layer close to the limitans (Figs. 62, 63, and 64).

Significance and Distribution—Where the photomechanical changes are as complete as described above, and carried out smoothly and within an hour's time or less, the whole machinery is clearly of great value in adjusting the retina to the external illumination. The workings of the Duplicity Theory are beautifully seen in these phenomena, for the cones are most advantageously placed for action in bright light, the rods being then shielded from excessive stimulation (or from any at all); and in dim light the rods are fully exposed while the cones get out of their way, whether this latter happening has any obvious value or not. As a device for equalizing the actual stimulation permitted to the visual cells in various illuminations, the photomechanical system at its best is excellent and has only the single drawback of slowness. Even this defect may be unimportant in the case of an animal with sedentary habits and deliberate movements, for temporal changes in natural illuminations are rarely rapid. But the low speed of the retinal migrations would seem to be detrimental to an agile species which flits from light to shade sporadically and lacks any more rapid means of regulating the illumination of its visual cells. Among such forms would be fishes which move rapidly from the bright surface to the dim depths and vice versa, and those which inhabit coral reefs and the like, which may help to explain why the latter are commonly crepuscular.

Table II summarizes the occurrence and relative effectiveness of the photomechanical changes in the various vertebrate groups. The reader will note a general tendency for them to dwindle in importance as one passes from lower to higher forms, the reason for which will be discussed in Section C.

TABLE II — PHOTOMECHANICAL CHANGES

			HABITS AS TO LIGHT	PUPIL MOVEMENT	ROD MIGRATION	CONE MIGRATION	PIGMENT MIGRATION
FISHES	Cyclostomes (Lampreys)		most are diurnal	—	—	—	—
	Elasmobranchs		most are nocturnal	extensive, but extremely slow	—	(few cones at most)	(no retinal pigment)
	"Ganoids"	e.g. *Amia*	diurnal	slight and passive (when lens moves in accomodation)	+	+	+
		e.g *Acipenser*	nocturnal		?	?	(pigment clumped in scattered cells)
	Dipnoans and Cladistians		nocturnal, limicolous	+ in some	?	?	?
	Teleosts		various	only in eels, flat-fishes, stargazers, etc.	very rapid and extensive* (none in flatfishes, tho pigment moves)		rapid & extensive
AMPHIBIANS		Anurans	arhythmic or nocturnal	+	slight, but fairly rapid	fairly rapid, extensive	fairly rapid, extensive
		Urodeles	secretive	+	almost none	slight and slow	less, and slower, than in frogs
		Cœcilians	fossorial	?	?	(no cones)	?
REPTILES		*Sphenodon*	nocturnal	rapid & extensive	?	(almost no cones)	?
		Crocodilians	nocturnal	rapid & extensive	slight	and	slow
		Turtles	diurnal	slight & incidental (lens blocks pupil)	(very few rods)	very slight and slow	
	Lizards	Most	diurnal	slight	(no rods)	very slight and slow, if any	
		Some	nocturnal	very rapid and extensive	—	(no cones)	very slight and slow, if any
	Snakes	Most	diurnal	slight or absent	(no rods)	—	—
		Some	nocturnal	rapid & extensive	—	— (a few colubrids have no cones)	—
BIRDS		Most	diurnal	rapid & extensive (voluntary?)	?	fairly rapid and fairly extensive	
		Some	nocturnal		—		
MAMMALS			various	very rapid and extensive in most	—	—	—

* the eel is unique, in that its rods migrate and its cones do not

Immediate Causation—It is evident from the table that there are few important vertebrate types about whose photomechanical changes, or lack of them, we cannot make positive statements in a descriptive way; and the reader has just been promised an integration of the apparent hodge-podge of their distribution, and an interpretation of the phylogenetic degeneration of these ingenious phenomena. But there is no branch of physiology which is in a less satisfactory state than the whole matter of the immediate nature, causation, and control of the photomechanical changes.

The unwieldy literature of the subject is full of contradictory conclusions based on seemingly equally sound lines of evidence, on failures to take account of the great individual physiological variability of the lower vertebrates (particularly the amphibians!), and on simple ignorance of other workers' results, especially of conclusive negations of some of the pioneering researches.

We do not even know whether either extreme position of the retinal pigment or of the rod or cone myoids represents a condition of relaxation, or whether the expansion and retraction of the pigment and the elongation and shortening of myoids are all active processes. We can glibly say that the movements of the pigment are "due to protoplasmic streaming" but (though it could easily be ascertained on isolated epithelium *in vitro*) we do not know whether the pigment cell can respond in either direction, autonomously and directly, to light and darkness. We have no conception whatever of the intracellular mechanism which changes the length of a myoid, though these changes are enormously greater than those which take place in a striated muscle cell whose fibrillar machinery is fully revealed to microscopic view. And we are greatly puzzled by the fact that apparently the same stimulus, or lack of stimulus, which causes the myoid of one visual-cell type to elongate, simultaneously causes the other to shorten. It is known that myoid volumes remain constant at all lengths, and that shape-changes elsewhere in the visual cells are purely passive. It is known that contractile cone myoids respond by shortening in the presence of acids, and that retinæ which contain cones are acid in the light and alkaline in the dark. Studnitz has injected phosphoric acid into dark-adapted fishes and found that the pigment and cones took their 'light' positions. Injections of alkali into light-adapted fishes made them dark-adapt. Studnitz thinks that even the effects of adrenalin chloride are due to its acidity, not to the hormonal base. To what it is that rod myoids respond, and how, no

one can say. Contractile ones look no different from non-contractile; and there are such paradoxical situations as that in the frog, where the common 'red' rods, with stubby myoids, have a respectable migration while the scanty 'green' rods, with very long myoids like a teleost rod or a dark-adapted frog cone, move but little if at all (see Fig. 23, p. 55).

The photomechanical phenomena are interesting enough and baffling enough in their normal operation, but perhaps the most remarkable thing about them is that they may actually work better when out of their normal environment: it has been found that the pigment and cone movements become almost twice as extensive in a salamander eye which has been transplanted, in the larva, into the location of the ear!

As to the control of the movements, opinion is divided between two schools of thought. Most of the work—not all—on fish material indicates that efferent nerve impulses control the movements. Cutting one nerve to the eye may halt the migrations, and cutting another in addition may let them recommence. In one fish, the day-night rhythm of the retina is known to persist even in constant darkness; nor does a frog stay dark-adapted in darkness—in a few hours the cones elongate, then shorten.

Much of the reported work on amphibian material favors the idea of control by blood-borne substances. Nerve-cutting has little effect, vessel-ligation a considerable one. The transplanted eyes referred to above were entirely divorced from nervous control, but adequately vascularized. The effects of drugs, narcotics, and anæsthetics are ambiguous. The effects of temperature are especially mysterious, for both high and low temperatures cause light-adaptation in the dark and inhibit the dark-adaptation of previously light-adapted animals. Excised dark-adapted eyes will light-adapt readily, but excised light-adapted eyes will dark-adapt only in the surprisingly special environment of a second frog's body cavity. Emotional states interfere with the phenomena, but these could have their effects by means of either nerve-impulses or hormones. Yellow light is more effective than other colors, speaking either for a reflex control from the visual apparatus itself (as in the case of iris reactions in higher animals), or for a direct influence of acid, formed maximally in the retina under yellow light. On the other hand, old evidence—still commonly cited—for reflex effects from one eye to the other and from the skin to the eyes is under grave suspicion, for in the experiments the animal's breathing was interfered with and fear was introduced, by the employment of leather hoods. Either of these factors is now known to be enough to make a frog light-adapt, though he be in darkness.

The whole subject requires a very careful review and deserves the attention of at least one cautious investigator prepared to devote his active career to it. Practically everything which has been done in the way of experiments upon the mechanism of the phenomena needs repeating with better technique than has been used. Not a single experiment has yet been made with all factors controlled, nor a single graph plotted with nearly enough animals averaged at each point. The photomechanical changes are so fascinating that their students have been a little too impatient to know what makes them go.

(C) Pupil Mobility

Functions of the Pupil—The pupil ordinarily has two chief responsibilities. It must fix the immediate illumination of the retina, if it can, at a value above the threshold of stimulation and below the point of dazzlement or injury; and it must restrict the perceived light-pencil to the center of the lens as far as possible. The pupil may be relieved of one or the other of these duties. Thus in the chameleons the lids are fused to the surface of the eyeball and their opening is a small one which 'stops down' the broad lens without benefit of changes in pupil diameter. Again, a strongly nocturnal animal may so conduct himself that he is seldom or never exposed to bright light, and his wide pupil may not need, or have, much ability to close down, to convert a dazzling external illumination into a tolerable intra-ocular one.

Though not at all exceptional, such conditions are nevertheless associated with the extremes of diurnal and nocturnal adaptation and behavior. The pupil may have little to do in a night-prowling species which conceals itself well in the daytime and has no wish to bask in exposed positions. It may have little to do in a sun-worshipper whose pure-cone retina is so insensitive that various natural brightnesses above his threshold are about equally comfortable to him. The slit pupils, so characteristic of those nocturnal forms which do court the sunshine, deserve special consideration beyond the scope of this discussion (see Chapter 9, section C).

The need for considerable pupil 'excursion'—range of size change—is thus the greater, the more the animal attempts to attain twenty-four-hour visual capacity. In such animals the responsibility of the pupil and its controlling mechanism is greatest also, for the two aims of the pupil are increasingly at cross-purposes when the period of daily activity becomes longer and longer. In the brighter hours, the closure of the pupil

serves both of the aperture's functions equally well; but as the animal attempts to make use of the evening and night hours, or to set back the alarm-clock in the morning, the pupil must walk an increasingly precarious tight-rope. It must open far enough to permit of stimulation, but not so far that the blurring of the image takes more away from vision than the increased light confers. Fortunately, as the intensity falls very low, the widening pupil finally begins to add more to the quality of the image, in brightness, than it takes away, by aberration. As day passes into night, the now familiar acuity-sensitivity seesaw (p. 69) begins inexorably to move. In any but a very strictly diurnal animal, sensitivity goes up, perhaps very high; and in any and all animals, acuity inevitably comes down.

A highly mobile, precisely controlled pupil prepares its owner for both night and day. We have seen that the same can be said for a well-developed system of photomechanical changes. An active iris in a given animal may be free to give its whole allegiance to illumination, or its movements may be tied reflexly more closely to accommodation, convergence of the two eyes, or emotional changes, or may even be under the control of the will. The pupil may be so blocked by the lens that its closure is impossible unless the iridic sphincter is able actually to compress the lens (a possibility which, as an adaptation to amphibious habits, is realized in some vertebrates). In the majority of fishes, the blockage is so complete and the lens so firm or so large that any attempt at pupil movement is hopeless and the iris is actually devoid of muscle.

Pupillary versus Retinal Adaptation—Being more familiar with movable pupils, we are likely to think of the photomechanical changes in the retina as being able to save such situations, and take the place of extensive pupil mobility. Historically, it has really been the other way 'round; for as we saw in the preceding section, the phylogenetic history of the photomechanical changes has been one of fairly steady reduction from a peak in the teleosts to complete absence in the mammals, the birds being exceptional, since in them, despite their high position and their mobile pupils, the photomechanical changes have been resuscitated for special reasons which will later be set forth.

Concomitantly, there has been a steady development of pupil mobility—among twenty-four-hour and nocturnal animals—from nothing in most fishes to a maximum in the mammals. We may reasonably expect to find then, at any evolutionary level, one or the other of these regulatory mechanisms in good condition (consult Table II, p. 150).

A pure-rod animal may need neither photomechanical changes nor a mobile pupil, if he is content to be strictly nocturnal; and a diurnal animal will need neither very badly if he has a pure-cone retina and can afford to be blind in dim light and utterly dependent then upon other senses—as a pure-cone retina necessitates. But if a form whose retina is duplex is to be able to appear indifferent to depth of water or to night and day, or if a pure-rod animal is to be able to bask in comfort and to defend itself from an enemy which routs it out of its daytime slumber, it must have a widely excursive pupil *or* effective photomechanical changes. Only one other mechanism, of limited value and with primarily other functions, can sometimes be called into play for the regulation of stimulation: the lid apparatus—sometimes, as regards its awning-effect, substituted for by projections on the upper part of the iris. The importance of the lids in this connection can best be judged from instances in which they are absent. Thus for example in the rays, the vipers, and the geckoes, movable lids are lacking and the pupil is capable of an exceptional degree of closure as compared with relatives which do have functional lids.

We can expect to find that a pupil will tend to open unless something makes it close. The inherent elasticity of the connective-tissue stroma of the iris tends to insure this, and in some animals, notably certain small mammals in which a dilatator is lacking, it is the only antagonist of the sphincter. Where there is a dilatator, it is a thin sheet, but a broad one; and its total bulk compares favorably with that of the sphincter. One or the other may be the stronger in a given case; but the orientation of the dilatator, other things being equal, gives it a big advantage over the sphincter. It is as though the two muscles are pulling on opposite ends of a lever of the first class, the ratio of whose arms is 3.1416:1; for the sphincter, contracting around the periphery of a circle, must shorten π units while the radially-oriented dilatator relaxes one unit, and the sphincter cells must be capable of contracting π times as fast. Of course if a pupil can move at all it can both open and close; but it is sometimes more important for it to open in dim light than for it to close in bright. Where the pupil is static, it is even more necessary for a nocturnal animal to have a large one than for a diurnal animal to have a very small one, for the latter can always partly close his lids. Where it is mobile, it is more desirable for a nocturnal pupil to close promptly in bright light than for it to open so suddenly in dim light, where the accumulation of rhodopsin is very slow anyway. Hence it is that many a small nocturnal animal has a powerful sphincter muscle and no dilatator at all.

In emergency situations, in the higher vertebrates, the pupil seems to try to make sure of enough light—its response to pain, to rapid deep breathing, or to strong emotion of any kind is to dilate, sometimes so fast and far (as in the hyænas) as to seem to be under the animal's control. Close scrutiny of an object, ordinarily a calm and non-emergency procedure, is on the other hand accompanied by contraction. This 'accommodation reflex' is not a true reflex, but a fortunate accident of innervation. The iris sphincter and the ciliary muscle are supplied by the same nerves. The 'reflex', which in man occurs more with convergence than with the accompanying accommodation, and is in that aspect truly reflex, is of some value in all its possessors (though of most value in those vertebrates whose irides actually aid in accommodation; see Chapter 11, section C). In its accommodated form the lens has more spherical aberration. It therefore needs more stopping-down, and receives this upon the reflex closure of the pupil, thus increasing resolving power for approaching objects. As objects approach, the amount of light received from them increases enough to compensate adequately for any accommodatory reduction of the area of the pupil.* Another pupil reflex in man, of no obvious value, has recently been described: it consists of a slight contraction at the moment of fusion of the two monocular images into a single stereoscopic one, as when one is observing through a stereoscope.

In the birds, whose photomechanical changes are more conspicuous than one would expect from the phylogeny of the changes and of the pupil, the reason appears to be that the bird pupil pays less attention to illumination than to accommodation and emotion. The 'play' of the pupil of a captive wild bird will readily convince one of this, though the irides of tame birds, such as chickens, may react quite staidly to light. There is thus no inconsistency in the fact that the birds have both iridic and retinal photomechanical changes well developed (Table II, p. 150).

The behavior of the pupil is influenced more immediately, as well as in in the long evolutionary run, by the presence or absence of retinal migrations. The first reaction of a pupil (*i.e.*, partial closure) upon a sudden increase of illumination is not permanent. It gives opportunity for the retina to reduce its sensitivity; and when this has been sufficiently effected, the pupil slowly reopens to a size which is smaller than its original one, and is constant until a further great change in intensity. This physiolog-

*In the dog, according to Nicolas, the accommodation reflex works backwards—the pupil dilating for near, contracting for distant objects; and there is no consensual reflex. These peculiarities have yet to be explained.

ical adaptation of the pupil is to be sharply distinguished from the immediate reaction it gives to increased illumination. Upon a reduction of illumination the pupil only dilates to a new constant size, there being rarely a brief preliminary contraction. The rate of the complex light-adaptation and of the simpler dark-adaptation of the pupil depends upon the method by which the retina changes its sensitivity. When only cones are present, as for example in diurnal snakes, the change in sensitivity is slight and rapid and the pupil also makes quickly the slight adjustment of which it is capable. Where many rods (but no photomechanical changes) are present, as in the guinea-pig for instance, the light-adaptation of the pupil is governed by the relatively rapid destruction of rhodopsin. Where both rods and photomechanical changes are conspicuous the rhodopsin is more abundant and, especially in fishes and owls, slow to bleach. The pupil then adapts much more slowly (frogs) or not at all (fishes), since retinal sensitivity is altered primarily by the relatively slow pigment migration. It is in fact quite probable that in the teleosts the rhodopsin is seldom all bleached, since the rods are completely shielded by expanded pigment. Higher vertebrates, it would seem, must be able to form more rhodopsin since so much must be destroyed at every light-adaptation. Very likely, the greater instability to light of the rhodopsins of higher vertebrates (through which the rhodopsin is quickly destroyed, and the threshold of the retina as quickly raised) is partly a consequence of the lack of such perfectly protective photomechanical changes as the lower vertebrates possess.

Pupil movements are thus not only less marked, but less rapid, in primitive forms which still depend primarily upon retinal migrations. Phylogenetically there has been a steady perfection not only of the pupil as an adjusting mechanism, but also of its method of actuation and control. In the few fishes which have iris muscles, these are pigmented and respond directly and autonomously to light—the sphincter by contracting, the dilatator by losing tonus. These actions are extraordinarily slow—elasmobranch pupils take two or three minutes to close in bright light and an hour or so to re-open in the dark! Such muscles are unresponsive to electrical stimulation and to neurotropic drugs like atropin, since such agencies operate through nervous connections. In the amphibians and some reptiles some degree of autonomy persists, although in the intact animal it is masked by the superposition of a control through the nervous system by means of reflexes originating in the retina. In the frog it has recently been reported that an intra-ocular reflex occurs—the pupil of the

excised eye contracts somewhat if the retina is stimulated. In the higher vertebrates, at least in adults, reflexes alone are of importance although some direct response is known to occur even in two or three mammals and man; and emotional changes can now affect the pupil, though whether this is incidental or not, useful or not, is difficult to say. In the mammals, 'consensual' reflexes from one eye to the other appear: the movement of both pupils when only one is stimulated (known only in the rays and the pigeon, outside of the mammals); and the neurological tie-ups of the pupil to accommodation and convergence become rigid.

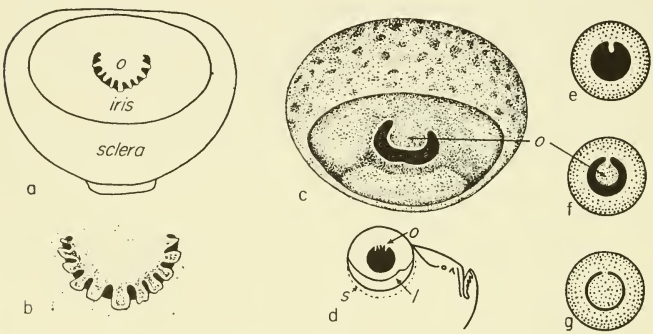

Fig. 65—Pupillary opercula in fishes (*o*- operculum).

a, eye of *Raja clavata*. × 2. After Franz. **b**, illuminated pupil of *R. clavata*. After Franz. **c**, eye of a flatfish, *Scophthalmus rhombus*, as seen from above. × 3. From Franz, after Grynfeltt and Demelle. **d**, upper part of head of stargazer, *Uranoscopus scaber*. × 4. Redrawn from Hein. *l*- lower 'lid'; *s*- limit of sulcus under lower 'lid'. **e, f, g**, stages in the expansion of the operculum of a loricariid catfish, *Plecostomus*. Redrawn from Roth.

Comparative Survey of the Two Methods—In the lampreys there are no iris muscles and most observers agree that the pupil is static. The lens touches the cornea and blocks the pupil, and the mechanism of accommodation (Chapter 10, section A) is such that this relationship is never changed. There are no photomechanical changes in lampreys; but their eyes as a whole are built for diurnality. When lampreys do swim at night, as when going upstream to breeding grounds, they are in all probability depending upon senses other than vision (like diurnal birds migrating at night).

The elasmobranchs are conspicuous among the fishes for having highly mobile (though excessively slow—*v.s.*) pupils. The sphincter is unusual and primitive in that it is never separated from the epithelium which generates it, as in other vertebrates. They have no retinal photomechanical changes—indeed, no retinal pigment except in the extreme periphery to which the tapetum lucidum does not reach. Most forms are active principally at night, but some like to doze, basking, at the surface. A few may be found active at any hour, and a considerable number live in the deep sea and are in a constant environment as regards light. The light-lovers have broadly elliptical, usually vertical pupils which dilate to circles in low illuminations. The more strongly nocturnal species have more mobile pupils which close in bright light to narrow slits set diag-

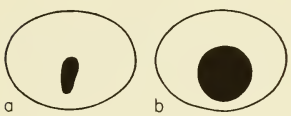

Fig. 66—Eye of a shark, *Squalus acanthias*, showing mydriatic pupil rigor. × 1. Redrawn from Franz.

a, when pupil is freshly illuminated.

b, after illumination of long duration.

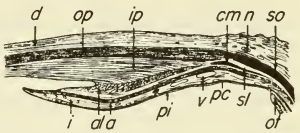

Fig. 67—Dorsal iris-angle region of a teleost, *Chrysophrys aurata*. After Grynfeltt.

a- argentea; *al-* annular 'ligament'; *cm-* ciliary muscle; *d-* dermal contribution to cornea; *i-* iris; *ip-* inner portion of primary cornea; *n-* nerve; *op-* outer portion of primary cornea; *ot-* ora terminalis; *pc-* pars ciliaris retinæ; *pi-* pars iridiaca retinæ; *sl-* suprachorioidal lymph space; *so-* scleral ossicle; *v-* blood vessel.

onally or horizontally. They are thus safe from dazzlement and defenselessness when they come up to sun themselves. The flattened, upward-gazing rays are provided with an 'operculum' which can expand to fill the pupil from within (Fig. 65). The electric ray or torpedo, however, relies upon a horizontal slit, which a tiny operculum can divide in the middle. The pupils of elasmobranchs need not necessarily hold their full contraction in bright light, but are privileged to reopen again after a time just as though photomechanical changes had taken place—for these fishes have photomechanical changes in the *chorioid* which alter the sensitivity of the eye (see Chapter 9, section D). Some sharks (*e.g., Squalus, Mustelus*) in fact develop a 'mydriatic pupil rigor' if kept for several days in a lighted room—their pupils become widely open and refuse to close down when additional light is thrown on them (Fig. 66).

The sturgeons are elasmobranch-like in habits as well as otherwise. Their pupils (*Acipenser fulvescens, Scaphirhynchus platorynchus*) are broad, pointed vertical ellipses or rhomboids, which appear to move only passively as the lens blocks or unblocks them (in accommodation?). The other chondrosteans, and the holostean fishes, have not been studied. The lungfishes have no iris muscles although one (*Protopterus*) has a mobile pupil. Here the contractility of the unmodified epithelial cells of the pars iridiaca retinæ seems to be involved, as possibly also in a few teleosts.

Among the teleosts only the eels and the flattened upward-lookers (*e.g., Uranoscopus* and *Lophius*) have much pupil excursion. The commensal pearl-fish, *Encheliophis* (=*Fierasfer*) *jordani,* also has the eyes aimed upward and is highly exceptional in that its pupils can close to a mere dot. Many of the flounders and their relatives, and one or two armored catfishes, have a pupillary operculum (Fig. 65). Most teleosts have no functional iris muscles whatever, though the non-contractile 'sphincter of Grynfeltt' is often present. In atypical eyes, like those of *Periophthalmus,* a functional sphincter may be present without a dilatator. The lens bulges far through the pupil except when pulled backward in accommodation, but does not necessarily actually block it, for in many species a narrow 'aphakic' (lenseless) space surrounds the lens. The teleost iris is usually so anchored to the cornea by the so-called annular ligament (more properly, 'iris angle tissue'—Fig. 67, *al*) that any iris muscles would be powerless to alter the pupil. In the minority which do have iris muscles (and weak annular ligaments) these are peculiar in that the dilatator consists of true, discrete muscle cells lifted free of the posterior epithelium and embedded, like the sphincter, in the stroma.

Most teleosts thus depend upon retinal photomechanical changes, which were evolved by these fishes or by their holostean ancestors. The retinal movements control stimulation well enough and the animal does not miss the stopping-down effect of a contractile pupil because of the peculiar optics of its eye. One would expect the spherical lens to have an excessive degree of spherical aberration and to need more stopping than the flatter lenses of terrestrial forms. But the teleost lens has a radially graduated index of refraction and the retina is a spherical surface, concentric with the lens. Hence the retina receives a sharply focused image from any angle and the eye is in effect both periscopic and aplanatic. Constriction of the pupil would serve no useful purpose. Indeed, the pupil margin need not overlap the lens at all; and the iris may even be lacking, as in

some deep-sea fishes (Fig. 84c, p. 213), the lens then being huge and filling the anterior chamber. The teleost pupil may close slightly in accommodation, probably passively due to its elasticity, when unblocked by the receding lens; but this is quite meaningless not only because the lens needs no differential stopping (being fixed in shape), but because the active accommodation of teleosts is for *distant,* not near, objects (see Fig. 98, p. 251).

The pupils of amphibians have more excursion than those of teleosts, though not as much as they would need if the amphibians did not have rather good photomechanical changes. Thus the frog, despite its potentially sensitive duplex retina and its extremely large rods (Fig. 64, p. 148), has a pupil identical in behavior with that of a pure-cone grass snake devoid of photomechanical changes. If the frog also lacked retinal photomechanical changes, his pupil would have to close farther than it does to permit him to be out where the snake could see him! A few anurans have peculiarly shaped pupils. That of *Bombina* contracts to a playing-card 'heart'; and in those whose retinæ are probably the most sensitive, the spade-foot toads (*Scaphiopus* spp.), the contracted pupil is a vertical lozenge, the playing-card 'diamond'. The two other suits of the deck are apparently not represented among amphibian pupils, but there are still other weird shapes whose meaning is quite unknown (Fig. 87, p. 223).

The weak amphibian sphincter pupillæ is replaced by a much more powerful one in the reptiles and here, as in birds also, the iris and ciliary muscles are of the *striated* variety. This change may have been inevitable upon the supervention of a control which is almost completely nervous and sometimes voluntary, though the return to smooth intra-ocular muscles in the mammals argues against this supposition. At any rate, the sauropsidan iris is capable of extremely rapid action, though particular species do not necessarily ever tax this capacity. The turtle pupil, fish-like, is blocked by the lens and does not respond to light at all, contracting only as an accessory to accommodation. Turtles have practically pure-cone retinæ with slight, slow retinal migrations or none at all. Their insensitive eyes require neither type of protection from strong light, and in turn limit their possessors to photopic vision and to dependence upon olfaction in dim light or muddy waters.

In diurnal lizards the iris is but slightly responsive to light, as is true also of diurnal snakes, some of which have quite motionless pupils. Nocturnal lizards are usually pure-rod, and nocturnal snakes are rod-

rich or even pure-rod. Many species in both categories are fond of basking, and the geckoes are often active in the brightest of light. This twenty-four-hour activity is made possible by great pupil excursions, which are perhaps exaggerated by the absence of movable lids. Thus, some geckoes if not most or all, and even one or two snakes (*Leptodeira annulata,* for example) can close their pupils completely. The gecko, with a large eye and retinal image, and a retina which, though pure-rod, often has excellent resolving power (since the rods are but little summated and owe their sensitivity to their size and to their rich content of rhodopsin) has probably the best allround, night-and-day eye of any vertebrate below the mammals.

The crocodile group is nocturnal. Its members, notoriously fond of basking, depend for the protection of their sensitive duplex retinæ upon the lids and pupil rather than the retinal photomechanical changes, which are here at a low ebb. Highly active pupils, among the reptiles, thus go with pure-rod and duplex retinæ and are the more mobile, the more the species or group scorns concealment in the daytime. The circular pupils of the diurnal majority are relatively or quite inactive, as would be predicted from their pure-cone retinæ.

Bird pupils are very active, but the photomechanical changes have made a phylogenetic 'come-back' in this group. The paradox is resolved when one notes the lack of precise adjustment of the avian pupil to illumination. It plays so much that, although experimental proof is as yet lacking, many workers have suspected it of being under the bird's voluntary control. At any rate, it is easy to understand why in the birds the retina has had to re-assume the responsibility of regulating its own stimulation—the pupil cannot be trusted to do so.

Mammalian pupils—except those blocked by enormous lenses in some strongly nocturnal forms (Fig. 71, p. 173)—are comparable in mobility with those of birds, but are better-behaved with respect to intensities and thus make retinal migrations quite superfluous. Excursion is greatest, of course, in nocturnal forms which love to bask, like the cats and foxes. It is reduced in many ungulates, and is least in crepuscular forms such as the bats, in secretive night-prowlers, and in such sun-worshippers as the ground-squirrels. In short, the more constant are the illumination-conditions in which a group prefers to be active, the less mobility the pupil exhibits. The pupil closes almost completely in *Tarsius, Pedetes,* dormice, and cats, very far in the otters and (by means of an operculum) in some whales. It has an exceptional range of movement in the seals—but not

primarily, strange to say, for the regulation of intra-ocular illumination. The unique physiological rôle of the seal's pupil will be found explained on pages 446-8.

In the mammals, the retinal photomechanical changes are entirely gone. In this group of vertebrates we see the end result of the evolutionary replacement of those older equalizing devices by the more rapid, hence highly superior, one afforded by the iris musculature.

(D) Duplicity and Transmutation

The duplex retina itself is clearly an adaptation for the extension of the seeing-period over a greater number of the twenty-four hours. Rods and cones are homologous *inter se,* and one type must have preceded the other in evolution; for, an intermediate type of visual cell partaking equally of the qualities of modern rods and cones is quite impossible of conception.

The accepted belief is that the rod is the more ancient and that the cone is an improvement upon it; but what real evidence there is points to the exact reverse of this view. The problem involved here reminds one of the question: "Which came first, the hen or the egg?" but it is not without theoretical importance in connection, particularly, with color vision. The evidence derives largely from the embryology of the visual cells as interpreted in phylogenetic terms. There is not space here to set it forth in detail, so the designation of the cone as primitive is bound to seem a little arbitrary.

Considering the flagellar origin of the outer segment (see Fig. 55, p. 127) the percipient parts of ancient visual cells must have been filamentous before they could have become massive, and we cannot imagine the pro-vertebrate to have possessed already so ingenious a material as rhodopsin or to have been anything but a strictly bright-light, pelagic organism. Until some of the visual cells became enlarged, and grouped in their connections to ganglion cells, there could be no increase in potential sensitivity which could release the animal from bondage to the sun; and until the invention of rhodopsin, there could be no visual activity by moonlight. But withal there must be no wholesale conversion of visual cells if the capacity for daytime activity was to be retained—else the animal would merely have succeeded in shifting the active period without substantially extending it. Improvements in the dioptric apparatus making it more and more desirable, for the sake

of form-perception, to retain cones as well as the newer rods, the duplex retina as we know it today finally crystallized in a condition which made it possible at last for an animal to become arhythmic if various considerations made that desirable. A mechanism for discriminating hues was probably added rather late as a refinement whose first purpose was far from the æsthetic one which color-vision seems, to our anthropocentric minds, to serve (see pp. 463-4).

Present-day pure-cone retinæ are thus no more primitive than pure-rod ones, for both represent the secondary discard of a cell type for the sake of extreme specializations—which, as always, demand in payment the surrender of plasticity. And, not only have various vertebrates at various times swung from twenty-four-hour capacity toward diurnality or nocturnality, but they have returned from one extreme through arhythmicity or crepuscularity and even gone on to the opposite extreme.

Wherever even a few cones have been retained in a rod-rich retina, or a few rods in an almost pure-cone one, manipulations of sensitivity need be only quantitative and are as readily carried out in evolution as an alteration of the ratio of white blood cells to reds. But where the ancestors of a given group retained only one visual-cell type, it might seem impossible for any descendants ever to produce the other. Exactly this has happened, however, and apparently far more often among the reptiles than in any other extant group. Historically, these were the first vertebrates to feel fully the strain of being highly active without benefit of a high body temperature. Not only were they deprived of the warmth of the ancient waters, but they were without the energy-saving buoying effect which a fish enjoys. A little exertion goes a long way when the weight of the body is supported by water, and the tenderness of cooked fish flesh, like that of the disused flight muscles or 'breast meat' of a chicken, is a reminder of the easy lives such muscles lead.

It is not surprising that in the first terrestrial groups (the stegocephalians and the reptiles) many sub-groups tended early to develop strong diurnality and pure-cone retinæ, counting upon the warmth of the sun to speed metabolism to a degree which would permit of athletic agility in the search for food. Moreover, diurnality was an especially safe habit because of the temporary paucity of enemies on land. But the reptiles have had their heyday and have perforce yielded their place in the sun to the more successful birds and mammals. Most reptiles are still strictly diurnal, but as their enemies have multiplied and their average size has steadily decreased since the days of the dinosaurs, many

have come to be grateful for the shield of night over at least a part of their activities.

To regain a duplex retina and twenty-four-hour capacity—let alone to go still further on into nocturnality, loose or strict—the pure-cone reptiles have had actually to convert or transmute some or all of the cones into low-threshold, massive, cylindrical elements. In most cases these have been able to re-invent rhodopsin and thus fully deserve to be called rods. Intermediate stages in these transmutations can be seen in living species, which show us therefore some of the steps by which the original duplex retina may have come into being in the earliest vertebrates. The conversion of a diurnal reptile into an arhythmic or nocturnal one may be illustrated by considering a series of snake species which, though quite unrelated to each other, each exhibit a stage of adaptation through which the subsequent members of the series must once have passed.

All round-pupilled snakes have only cones, of three types as shown in Figure 26a (p. 63). Two of these are single, one large and abundant (Type A), the other small and scanty (Type C). The third is the unique double cone (Type B) invented by the higher snakes to replace the lost double cones of their lizard antecedents (see Fig. 24, p. 59).

In *N. natrix,* for example, these cone types are normal and typical. *Cemophora* is a secretive snake in which the Type A and Type B outer segments have enlarged, thus lowering their thresholds; but the biggest change is in the Type C elements. These are no more numerous than usual, but they have become rod-like in form (Fig. 68a).

The mud-loving and secretive rainbow snakes, *Farancia* and *Abastor,* maintain the large cone outer segments, and in them the numbers of the stubby Type C rods have increased until they equal or exceed the total number of "A" and "B" cones. The Type C elements probably still lack a rhodopsin at this stage of transmutation.

Any pit-viper, such as *Agkistrodon,* shows the next logical steps. The rods have multiplied until they have a human-like abundance relative to the cones (Fig. 68b), and they are longer than in the rainbow snakes and now contain rhodopsin. With this retina, and a small eye with a small, bright image, the pit-viper has enough sensitivity to require considerable pupil mobility, and the animal can prowl at night and bask in comfort and safety in the daytime, sometimes even feeding actively then.

From the perfected duplex retina attained in the pit-vipers, among many others in which this same secondary adaptation to day-and-night

vision has occurred, still further steps may be taken. Thus in *Leptodeira* the rods are very numerous, long, and slender, and the bodies of the cones have gotten up out of their way, their ellipsoids being perched on the tips of the rods like so many pumpkins on a picket fence (Fig. 69). The cone outer segments themselves are very much larger than in pure-cone diurnal forms like *N. natrix, Coluber,* etc. Rhodopsin is abundant in *Leptodeira,* and the retina is so sensitive that the pupil closes completely like that of a gecko. In *Tarbophis* and *Dasypeltis* the

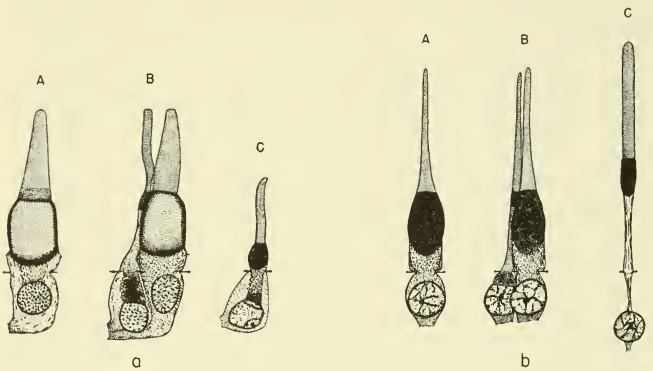

Fig. 68—Transmutation in snakes. × 1000.

a, visual-cell types of a secretive colubrid, the scarlet snake, *Cemophora coccinea.* Compare Figure 26, p. 63. Types A and B have enlarged outer segments, but Type C (which is greatly outnumbered by A + B, as in diurnal forms) is the most rod-like of the three.

b, visual-cell types of a crotalid, the copperhead, *Agkistrodon mokasen.* Types A and B have remained cones, but Type C (which greatly outnumbers A + B) is a perfect rod and contains a rhodopsin.

cones seem definitely to have lost importance, for while they are still elongated far beyond the usual position, their bodies and outer segments are much reduced in size as compared with *Leptodeira.* In these three genera (as also, it happens, in the flying-squirrels) the visual cells are in a condition of 'permanent dark-adaptation' (in terms of the photomechanical changes, which do not occur in snakes or squirrels) and the animals are strongly nocturnal—thus really lying beyond the scope of this chapter though serving to show the lengths to which a species can go, if it must, to change its habits and their structural basis.

There are other cases in which nearly all (*Sphenodon*) or absolutely all the cones of a pure-cone forebear have been transmuted into rods; and the result is not necessarily a strictly nocturnal animal, for the pupil

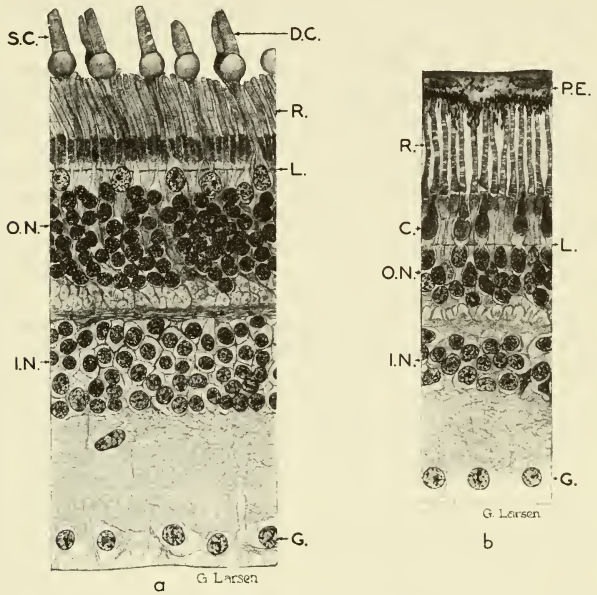

Fig. 69—Duplex snake retinæ. × 500.

a, a nocturnal colubrid, *Leptodeira annulata,* whose rods (derived by transmutation from the Type C cones of a diurnal ancestor—compare Fig. 26) are very numerous, and whose cones have taken a position which, in terms of the photomechanical changes of lower vertebrates, might be called one of permanent dark adaptation.

b, for comparison, a boïd, *Tropidophis melanurus,* whose simple, duplex retina is more ancient than the cone-simplex one from which the *Leptodeira* pattern was evolved.

C.- cone; D.C.- double cone (= Type B); G.- ganglion-cell layer; I.N.- inner nuclear layer; L.- limitans; O.N.- outer nuclear layer; P.E.- pigment epithelium; R.- rod; S.C.- single cone (= Type A).

is so well developed in some reptiles that it can often make possible twenty-four-hour activity even when, behind it, lies a pure-rod retina. Round-pupilled lizards have only single and double cones, which in

Xantusia have enlarged their outer segments and lost their oil-droplet pigment. The geckoes have still further enlarged the outer segments, discarded the colorless oil-droplets, and re-invented rhodopsin. In *Coleonyx,* for example, the transmuted rods are enormously long cylinders (Fig. 25, p. 62) and, though sensitive in the extreme, are adequately protected by the slit pupil from dazzlement in the daylight. At the same time, the rods of *Coleonyx* are slender enough, and little-enough summated, to afford respectable visual acuity. Thus *Coleonyx* has been able to become arhythmic by installing a hinge in the middle of the sensitivity-acuity seesaw. The geckoes can be comfortable in bright light with a pure-rod retina, while their diurnal lizard relatives, with pure-cone retinæ, are completely blind in dim light. It may be a little clearer now, why diurnality is a more restrictive habit than nocturnality; for while a pure-cone animal cannot see anything, even hazily, at night, a duplex or even pure-rod species can always see in the daytime, though perhaps not acutely—the real danger being that he will see too *much* light (bats, owls) if his share of photomechanical changes, pupil mobility, or lid apparatus is unable to reduce the stimulation of his rods to a comfortable value.

Pure-rod snakes, as well as lizards, exist by virtue of transmutation. A few pure-cone ones (*e. g. Lampropeltis, Rhinocheilus*) have increased sensitivity somewhat by enlarging the outer segments, eliminating color-filters (yellow lenses), and by hooking up more cones to each optic nerve fiber. *Arizona* and *Trimorphodon* have carried these processes so far that their pupils have had to become elliptical, and in *Hypsiglena* and *Phyllorhynchus* (Fig. 26b, p. 63) the visual cells are all morphologically rods though devoid of rhodopsin. When we can observe so clearly the secondary, apparently easy derivation of unquestionable rods from indubitable cones, it becomes easier to understand why both of these so diverse cell-types are usually required for a well-rounded visual capacity. And, it is a little easier to see that in order to become duplex, and thus more widely useful, the cone-like receptors of the provertebrate retina could spawn rods without necessity of their having to be formed *de novo* from a separate cellular ancestor. The first rods in the world were produced by the transmutation of cones, and the process has been occasionally repeated, wherever needed, ever since the vertebrates came on land.

Chapter 8

ADAPTATIONS TO DIURNAL ACTIVITY

(A) Diurnality and the Eye

Diurnality and Sharp Vision—The adoption of diurnality entails a sacrifice of sensitivity. This is hardly possible without a marked increase of visual acuity, for if the cones are multiplied at the expense of the rods, resolving power inevitably rises. While it is theoretically possible for an animal with a pure-rod retina and crude vision to be strictly diurnal, given the right type of pupil, in actual fact it never happens.

Adaptation to diurnality is thus, at the same time, adaptation for sharp vision. Diurnal animals are relatively keen-sighted, and their other habits are such as to demand keen sight; but it is of course impossible in most cases to say whether they are diurnal and cone-rich in order to have sharp vision (which is probably true of the birds) or have only cones simply in order to be diurnal, without making the most of the opportunity to gain sharp vision (which may hold for the snakes). The relationship between visual acuity and diurnality, in so far as it expresses needs and the production of adaptations to fill those needs, is perhaps most easily seen in a rough analysis of feeding habits:

Diurnality, Acuity, and Food—Animals which feed upon small objects such as seeds and insects must be able to resolve them, which is possible only for an eye rich in cones and hence diurnal in capacity. Most lizards, birds, and primates are in this category; as are also the tree-shrews, at least, among the insectivores. It is important to remember that insects themselves are poikilothermous, hence most species are most active and available under diurnal conditions. Nocturnal insect-feeders can place no reliance upon vision, but must either rely upon hearing and touch for securing individual insects (bats) or else 'trawl' blindly through the air for flying insects with wide-open mouth (goatsuckers, frog-mouths). The dependence of most birds upon sunlight is proverbial. So is their visual acuity. In this respect, man acknowledged even the small birds to be his superior, centuries ago—it was the habit of the medieval falconer to carry a caged shrike on his saddle, to keep track of the falcon. As long as the shrike acted fearful and excited, the hawker knew that his proud tiercel was in sight—though not to *him*!

Poikilothermous vertebrates, generally, may be diurnal for the sake of the activating effect of sunlight upon metabolism and locomotor activity, unless they happen to be particularly defenseless or especially dependent upon prey which in itself is nocturnal. Predaceous fishes, most reptiles, and some frogs fall here.

Predaceous vertebrates, generally, require fairly sharp vision at relatively close range in order to pursue and capture prey and obtain a grasp upon it which will be advantageous to them in any ensuing combat. Being ordinarily swifter than the prey—at least for short bursts—there is added need for acuity of vision, which must keep pace with speed if 'crashes' are to be avoided. These factors are especially operative in fishes, lizards, and birds; and they are largely responsible for the acuity-adaptations tenaciously retained by those carnivorous mammals which attempt to compromise between sensitivity and acuity by having large eyes. Small, small-eyed carnivores on the other hand are nocturnal, largely because the small prey animals which they are able to master have taken refuge from them in nocturnality.

Defenseless, herbivorous prey animals which rely upon speed for escape must recognize enemies at a distance. This in itself demands high visual acuity; and the factor of distance, besides reducing the retinal-image size of the potentially dangerous object seen afar, greatly reduces its brightness. Vision at a distance is therefore altogether impossible in dim light. The ungulates, and the more strictly diurnal mammals, must have high visual acuity for safety, and their acuity-devices will work only under bright-light conditions. Lastly, predators which specialize on diurnal prey must ordinarily be permanently or temporarily diurnal themselves—the hawks, for example, as also the bear during his annual gorge on salmon.

However, we must not suppose that in every act of predation both parties are under optimal conditions and fighting to best advantage. On the contrary, many a predator is nocturnal in order to seek out prey which, being itself diurnal, is asleep at night and hence at a disadvantage. Conversely, the diurnal predator may depend not upon diurnally active food animals, but upon nocturnal ones which, sleeping in their burrows by day, are then easily surprised and subdued. The diurnal snake exploring the nests of slumbering rodents, the nocturnal marten investigating a squirrel's dray, are examples of these advantageous employments of the sleep-time of the victim.

We can easily imagine that diurnality and nocturnality have come and gone, sometimes repeatedly, in particular lines of descent. Prey animals

have become nocturnal to avoid predators. Predators have in turn become nocturnal to continue to find food easily. To escape the nocturnal predators, prey animals have again become diurnal. Those species and groups which could not invert their habits at need were doomed unless, by sheer weight of numbers, by phenomenal fecundity, they were able to compensate (as species) for the enormous losses of ill-equipped individuals.

The Eye as a Whole—For an eye to mediate sharp vision, an essential requirement is a large retinal image. The greater the number of visual cells over which the image is spread, the greater the resolution of the details of the image. The histology of the retina is a very important factor but, after all, it can only say the *last* word in the story the eye tells the brain. There are strict limits to the fineness of the receptor mosaic, and its performance is in turn limited by the size of the image presented to it by the dioptric apparatus.

The simplest way to gain a large image is to have a large eye; and 'large' here refers to absolute, not relative, size; for whereas with other organs of the body it is relativity to each other that determines adequacy of size, the eye is essentially an optical instrument and obeys the laws of inter-organ proportioning only grudgingly, disobeying them entirely whenever, with impunity, it can. Biologists tend to overlook this fact, and frequently remark of large animals, such as the whales, that "their eyes are so small in proportion that they must be just about useless"—forgetting that the world looks the same size to a whale, a man, and a mouse. They all see as *much,* but not as *well.* Were a squirrel as big as a horse, it would have an eye as big as a horse's; but that is not to say that if a horse were as small as a squirrel, it would see as well with an eye proportionately small. The squirrel would, on the other hand, be much better off with eyes as big as a horse's—if it had room for such eyes in its head.

The big reason for this fact—that it is absolute rather than relative size which, *ceteris paribus,* determines visual acuity—is that the absolute dimensions of retinal elements vary within only narrow limits however large or small the eye may be. Tripling the diameter of the eyeball does not entail tripling the diameter of a cone visual cell. Rather, it results in a tripling of the number of visual cells in a given linear distance on the retina. The image is then three times as broad, and visual acuity is enhanced threefold.

In practice it is only exceptionally that high visual acuity can be gained

merely by having a large eye whose parts are proportioned as they are in small twenty-four-hour eyes. It is only in large animals such as the ungulates and the great cats that we find high visual acuity attributable principally to large ocular size as such.

Where the habits of the animal demand that he go all out for visual acuity, we find the eye to be large both absolutely and relatively. Thus in the birds the eyes are proportionately colossal and occupy so much of the head (Fig. 70) that their fundi may actually roll upon one another in

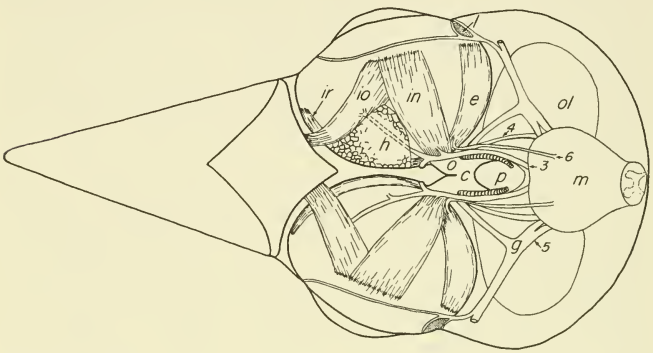

Fig. 70—Eyes and brain of the English sparrow, *Passer domesticus*, in situ, from the ventral side. × 5¼. Redrawn from Wood and Slonaker.

c- optic chiasma; *e-* external rectus; *g-* Gasserian ganglion; *h-* Harderian gland; *in-* inferior rectus; *io-* inferior oblique; *ir-* internal rectus; *l-* lacrimal gland; *m-* medulla; *o-* optic nerve; *ol-* optic lobe (midbrain); *p-* pituitary; *3-* third cranial (oculomotor) nerve—supplies the superior, internal, and inferior recti and the inferior oblique; *4-* fourth cranial (trochlear or pathetic) nerve—supplies the superior oblique; *5-* fifth cranial (trigeminal) nerve, several of whose branches carry fibers to the eye and adnexa; *6-* sixth cranial (abducens) nerve—supplies external rectus.

the mid-plane of the skull, like a pair of segmental gears. Only in species of little brain can such things be.

The partial dependence of resolving power upon absolute ocular size has a consequence upon relative ocular size. It has been stated as a law that eye size is inversely proportional to body size (Haller's ratio). The reason why this should hold for *nocturnal* forms as well as for diurnal ones will be given in the next chapter; but it is a very different reason. Keeping only diurnal forms in mind, it is easy to see why the eye should

be relatively large in, say, small birds and yet relatively small in such an animal as the horse. Though the horse has larger eyes than any other land mammal, there is ample room for even such large eyes in the head. The small bird must give over a far greater proportion of the head to the eyes if they are to be large enough in actual measurement.

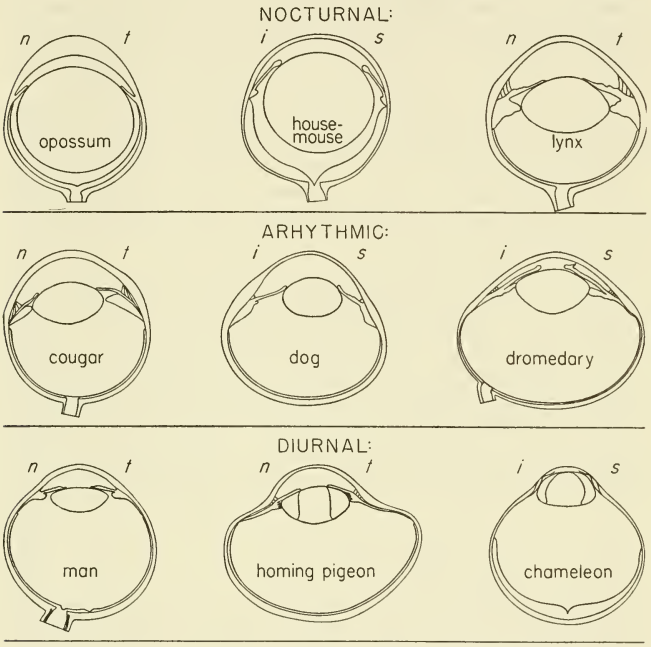

Fig. 71—Intra-ocular proportions in relation to intensity habits. Redrawn from various sources.

i- inferior side of eyeball; *n*- nasal side; *s*- superior side; *t*- temporal side.

Another factor which, by operating upon actual ocular size, has its effect upon relative ocular size, is locomotor speed. Great speed demands high resolving power for better perception of movements and for the avoidance of collisions (Chapter 10, section E); and this calls for a large

eye. In predaceous fishes, lizards, birds, ungulates, squirrels, and other swift and agile forms, large eyes go with swiftness of movement (Leuckart's ratio).

Wherever the eye of a diurnal animal is actually small it may be that visual acuity is low because, considering the animal's habits and needs, it need not be any higher. This is the situation in the snakes. Far more often, the eye is small because there is simply no room for a larger one. Internal adaptations then appear, which compensate for inadequate size; and the same adaptations occur in even very large eyes, supplementing the effect of size *per se,* wherever maximal visual acuity is desired.

These internal rearrangements usually consist at least of a flattening of the lens and a shallowing of the anterior segment of the eyeball. (It should be remembered that the anterior segment is not defined as the anterior *half* of the eyeball, in front of the equator, but as the portion anterior to a plane tangent to the back surface of the lens. This may comprise very much less than half of the volume of the eye). These changes have taken place in the birds and are perhaps most marked in the chameleon and in the higher primates (Fig. 71). The squirrels are conspicuous for having more nearly spherical lenses than other strictly diurnal vertebrates. The human eye, among mammalian eyes in general, is atypical in the other direction, in its possession of so very flat a lens. One gets the impression from the human, as also from most bird eyes, of an ordinary-sized anterior segment grafted onto an oversized posterior segment which 'doesn't belong' to it. This impression is actually quite true to the facts, for it is not that the parts of the anterior segment have been made smaller in order to gain visual acuity, but rather that the fundus of the eyeball has been made larger, the lens then flattening in order to move the focal level back onto the now more distant retina. The fishes are peculiarly fortunate in that they are able, because of the extraordinarily high refractive index of the lens, to obtain a broad image without the eye having to be as deep as it is broad. The fish eye is consequently flattened (Fig. 77b, p. 185) and encroaches less upon the internal structures of the head.

The effect of this alteration of the relative size of the anterior and posterior segments is to move forward the nodal points of the dioptric system. The distance from the optical center to the retina being thereby increased, the image enlarges just as it does when we draw a stereopticon lantern farther away from its screen. For the greater distance of 'throw' of the image, the lens must now bend the light-rays less sharply if they

are still to focus on the retina; hence the reduction of its sharpness of curvature. If we imagine the acuity-requirements of an animal to be steadily increasing through evolution, we may visualize the consequent gross changes in the eye thus:

1. A steady increase in absolute size until the eye is relatively large if the animal is small. If the animal is large, the eye may then still be relatively small though absolutely large. The result is an enlargement of the image and an increase in resolving power since the visual cells do not enlarge proportionately, but instead become more numerous per angular unit of the image.

2. A faster growth of the fundal portion, the anterior segment becoming, more and more rapidly, relatively small as compared with the posterior. The result is an increase in the size of the image relative to the size of the eye, with a consequent increase in resolving power.

3. A relative or an absolute forward movement (or both) of the optical center of the cornea-lens system, further expanding the image owing to the increased distance from optical center to retina (Fig. 71).

4. A relative diametral shrinkage and flattening of the lens or the cornea (or both), increasing the focal length to suit it to the increasing distance from optical center to retina.

5. A relative diminution of the size of the pupil and of its excursion of movement, there being abundance of light entering the eye under diurnal conditions (so that the pupil can be small) and, in the pure-cone retina in which diurnality tends to culminate, a restricted range of sensitivities (so that there is no point to having the pupil capable of opening very widely or of closing extremely).

(B) The Diurnal Retina

Cone:Rod and Receptor:Conductor Ratios—The diurnal retina is invariably rich in cone-substance. This clumsy term must be used in at least this one place, for the sake of emphasizing that it is the relative total *masses,* not the *numbers,* of cones and rods which count in retinal adaptations to sensitivity. For, an animal may have dozens of rods to every cone and still be suited best for diurnal activity—if the rods are tiny and the cones massive. This is actually the case in the bright-light teleost fishes (Fig. 22b, 23c, p. 54). Apart from them, the rule is that relative numbers of cones-per-rod are high in diurnal forms, low in nocturnal. And *within* the teleost group, this rule of numbers of course

holds. Wunder made counts in a number of species, and found the greatest number of rods (810,000 per square millimeter of retina) in the nocturnal *Lota*. *Lota* also had the fewest cones (3400/sq. mm.), the diurnal *Tinca* the most (9000/sq. mm.). The catfishes, however, have thick rods in their crude eyes. Wunder found no other teleost with so few rods as *Amieurus* (18,400/sq. mm.), whose rods are almost amphibian in plumpness (*cf.* Figs. 63 and 64, pp. 147-8).

The most strictly diurnal vertebrates have only cones in their retinæ. Among these are the great majority of lizards and snakes (all of those with round pupils), some (perhaps many) birds, and the majority of the members of the squirrel family—at least, the marmotines (ground-squirrels, prairie-dogs) are certainly pure-cone, and all others except the flying-squirrels are probably pure-cone.

In many birds, only a few rods can be found and these may be present over only a part of the whole retinal area. Cones outnumber rods very greatly in all diurnal birds which have any rods at all. Turtles have very few rods among their cones, and some species may have none. In freshwater lampreys, the cones and rods are equal in numbers; but in marine species the rods are more numerous to give the added sensitivity demanded by deeper water.

The most nearly diurnal of the amphibians—the frogs—have much higher cone-to-rod ratios than do some vertebrates which are more strictly diurnal than they; but in the amphibians the rods are so large and the cones so small that we have here a situation which is the reverse of that in the teleosts. The actual effect is of a preponderance of rods—just as in teleosts, with the rods very numerous but very tiny, there is an effective preponderance of cone-substance.

Except for the vertebrates above-mentioned, none is known to exceed by very much the cone-to-rod ratio of man, which is about 1:20 and seems very low—until we take account of the great size of the eyes of primates, large carnivores, and ungulates, whose retinal image sizes are such that many rods may be allowed to leak in between the cones without the visual acuity being pulled down below that of a small bird whose retina is pure-cone and whose cones are contiguous. Thus, where an animal has room for a large-enough eye, he can afford to have a duplex retina without sacrificing too much visual acuity, and then has the opportunity of seeing something in twilight or moonlight, whether he takes the opportunity or not. Most do—and thus it is that ungulates, large carnivores, and primates are able to stay up after the birds have

gone to bed, and tend toward twenty-four-hour activity. The presence of enough rods to make this possible would sometimes affect visual acuity too adversely, except for the development of a small *pure-cone* area, the 'area centralis', in the otherwise duplex retina. Such an area, like the whole of a pure-cone retina, is necessarily blind in dim light.

The outer nuclear layer, formed by the rod and cone nuclei, tends to have few rows in diurnal retinæ. Cones being usually more plump than rods, there is more room for their nuclei to lie directly against the ex-

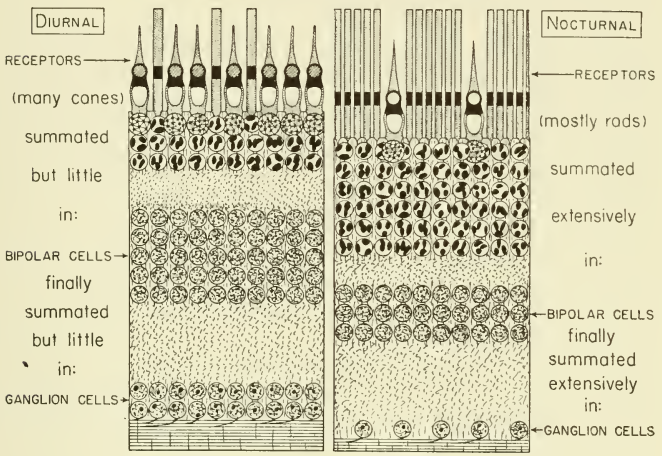

Fig. 72—Diurnal and nocturnal retinæ contrasted.

The diagrams represent two related species, one of which is diurnal and the other nocturnal. The characteristic differences in the relative thickness of the nuclear layers are the result of the visual-cell patterns and the differing extents of summation in optic nerve fibers.

ternal limiting membrane. Where rods are few or absent, this makes for a thin outer nuclear layer. In some lampreys, there is but a single row of nuclei. Turtles and squirrels have but a couple of rows, as do the amphibians—in the latter it is the unusual bulk of the rods, and their relatively small numbers, which is responsible. Where the rods are slender and are as numerous as they are in man, the outer nuclear layer becomes thick; and (Fig. 69a) it becomes far thicker still, of course, in twenty-four-hour and nocturnal eyes (except, again, in amphibians).

Where the cones are slender, hence numerous per unit of retinal area, their nuclei pile up in several layers. This is true in lizards and particularly in birds; and in all cases, in the pure-cone spots in duplex retinæ referred to above and treated at length in the next section. The snakes are quite conspicuous, among pure-cone forms, for having single outer nuclear layers—the reason being that the cones are generally fatter than their own nuclei (Fig. 68), since only a few snakes (*e.g., Dryophis, Malpolon, Sepedon*) have taken advantage of their diurnality to obtain high visual acuity by slenderizing their cones.

Though the outer nuclear layer tends to be thin, the inner nuclear and ganglion layers tend to be thick in diurnal animals. This is an expression of the reduction of summation (see pp. 47, 67), of the increase in the number of neurons per number of visual cells, for the preservation of the high resolving power which the multiplication and slenderization of the cones tends to produce. A diurnal retina can thus often be distinguished at a glance from a nocturnal one, for in the former the inner nuclear layer is usually thicker than the outer, this situation being reversed in the nocturnal retina (Fig. 72). A considerable portion of the characteristic thickening of the inner nuclear layer of diurnal retinæ is due to the greatly increased numbers of horizontal and amacrine cell-bodies; for, as diurnality is adopted and perfected by a vertebrate group, these integrative cells are multiplied even faster than the straightforward conductive ones (bipolars and ganglion cells) and may, as in birds, come to outnumber the latter. Though it would seem that ganglion: bipolar:visual-cell ratios would take up and finish the job of fixing visual acuity where the size and quality of the image and the concentration of cones leave off, the 'switchboard' effects of the horizontally integrative neurons have a mysterious and very considerable concern with the sharpening of the mental picture, probably by manipulating contrast phenomena. This particular specialization makes the bird retina the thickest of all—though it should not be thought that the variation of retinal thickness from group to group of animals is a very great one, for it is surprisingly slight.

Minimization of the Physiological Scotoma—The 'blind spot' of the retina may, in thoroughgoing diurnal eyes, be called upon to modify itself in sympathy with the efforts toward improving detail- and form-perception. The insensitive head of the optic nerve, called the 'disc' from its usual appearance when seen with the ophthalmoscope, causes

a physiological (normal) scotoma or gap in the visual field within which nothing can be seen. We humans are not aware of our blind spots, for since the two retinal topographies are mirror-images of each other and both are aimed forward, any object whose image falls within the disc of one retina is simultaneously imaged upon functional retina in the other eye. We are not even aware of the blind spot when one eye is kept closed, and can demonstrate it to ourselves only in an experiment such as is shown in Figure 73. An animal whose eyes are on the sides of his head, however, might as well have one eye closed so far as concerns what the other fundus is seeing; and hence he cannot fill in, with each eye, the blind spot of the other.

The blind spot becomes a serious matter only where the disc is relatively large; but this happens to be inevitable when the eye is especially well adapted for diurnality. For, it will then have a preponderance of cones, and the consequent great numbers of ganglion-cell axons make for a relatively heavy optic nerve and a large disc. On the other hand,

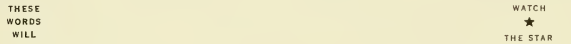

Fig. 73—Demonstration of the blind spot.

Cover the right eye; fixate the star steadily and move the book slowly toward and away from the face. The words at the left will disappear and reappear as their image swings on and off of the head of the left optic nerve.

the disc of a mouse is a mere dot, for each of the few optic nerve fibers is connected with hosts of rods.

In three diurnal assemblages the disc has become a narrow, greatly elongated oblong: in the squirrels, the birds, and the predaceous pikes, salmonoids, and percoids among the teleost fishes. Elsewhere it is usually circular but it may be oval, reniform, triangular—always, however, compact. A fatally large, compact disc has been avoided in the fishes by permitting the developing optic nerve fibers to fill in the whole length of the embryonic fissure of the optic cup, instead of massing them at the apex of the fissure (see p. 108) as other vertebrates do. The optic nerve thus often departs from the fish eyeball as a ribbon rather than a cord, and becomes crumpled edgewise to gain a circular cross-section between

eye and brain (Fig. 105e, p. 261). In the birds, the stripe-like disc is concealed under the base of the 'pecten', a pleated fin of pigmented, highly vascular tissue which arises embryologically from the lips of the embryonic fissure and projects lens-ward through the vitreous (Fig. 80, p. 188). The birds thus have only one narrow scotoma where they might have had two if they had located the pecten elsewhere.

The squirrels exhibit the most remarkable of all modifications of the disc (Fig. 74). It is a stripe, oriented horizontally to interfere minimally with the perception of vertical contours which are so important to an arboreal animal. It has been moved far above the optic axis whereas in other vertebrates it is almost invariably located close below the axis or even on it, in the center of the fundus. Since it is the lower part of the

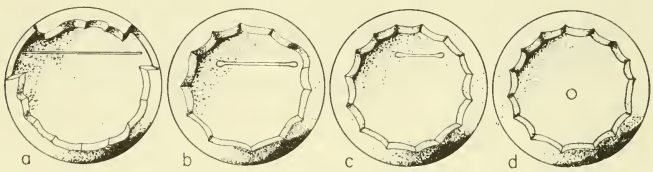

Fig. 74—The optic disc in various members of the squirrel family.

(In schematized views of the fundal portions of left eyes, the anterior segments being cut away; the drawings are not to the same scale).

a, prairie-dog, *Cynomys ludovicianus* (inhabits open spaces, very bright light). b, woodchuck, *Marmota monax rufescens* (inhabits less bright places). c, gray squirrel, *Sciurus carolinensis leucotis* (inhabits dense woods). d, flying squirrel, *Glaucomys v. volans* (nocturnal, with a nearly pure-rod retina).

retina which looks upward, vision of the sky, where the squirrel's chief enemies soar, is thus left unimpeded. The stripe-like disc is so slender that it bites out only tiny bits of vertical lines; and a tiny head or eye movement, up or down, will move any horizontal line off the disc and onto functional retina. Where the number of optic nerve fibers varies from species to species, the stripe varies in length (but not in width), in sympathy with the species' preference for bright light—from 78% of the diameter of the eye in the sun-worshipping ground squirrel down to 30% in heavy-timber tree squirrels and even less in the European squirrel (where also it widens somewhat), which seeks the darkest woodlands. The palm squirrel and the nocturnal flying-squirrels, as might be expected, have perfectly orthodox small, circular discs located just below the center of the fundus.

(C) Areæ Centrales and Foveæ

The Area Centralis—An important feature characteristic of the best-adapted diurnal eyes, and found in many twenty-four-hour eyes (as an adjunct to their diurnal activity phase) is the area centralis. It is best defined as a circumscribed retinal area within which the retina is so constructed as to afford a marked local increase in resolving power.

The name 'area centralis' is not too fortunate, for the area is not necessarily near the center of the fundus—though it happens to be in man, whose morphology has greatly influenced all anatomical terminology. In the human and other primates, the macula lutea (=yellow spot) of the retina is synonymous with 'area centralis', but the term 'macula' is most improperly applied to the areæ of other vertebrates. Similarly, the word 'fovea' is often badly misused, and it will be well to get these three terms firmly and accurately in mind:

An area centralis is only exceptionally pigmented, making of it a yellow spot on the otherwise colorless retina. Only then can it properly be called a macula lutea. This latter term should consequently be reserved—if, indeed, there is any need for it at all—for the areæ centrales of the higher primates, and possibly the chameleons. No others are known to have the diffuse yellow pigmentation of the inner layers of the retina in the area centralis.

Again, only certain areæ centrales have a depression or pit in the center; and it is just this pit, not the whole area, which should be called a fovea. An area centralis can occur without a fovea—it may actually be thickened, not thinned—but a fovea can exist only within an area centralis.

The various features of a full-fledged area centralis can best be set forth if we enumerate them as steps in the evolution of such an area in a hypothetical vertebrate. This animal must have taken on diurnality and—unless of course he eventually dispenses with rods entirely—must have a large-enough eye to be able to afford to devote a portion of the retina to an area centralis without sacrificing the ability to see in dim light with the greater part of the retina.

The first obvious thing to do is to increase, locally, the number of visual cells per unit area of the retina. This is brought about partly by making them more slender, partly by packing them more closely together than they are outside the area. Since the rods are like so much deadwood when it comes to affording highly-resolved images to the

consciousness, they are progressively eliminated and the area comes to be a pure-cone island in a duplex sea of unmodified retina.

As the rods are eliminated and the cones are aggregated and slenderized, the threshold of stimulation of the area tends to rise. The areal cones would then go out of action, in failing illumination, before the more massive extra-areal ones; but they counteract this tendency by evolving longer and longer outer segments. This local thickening of the visual-cell layer causes the external limiting membrane to bulge inward toward the vitreous, and may even make the pigment epithelium bulge outward against the chorioid ('fovea externa'). Retinal blood vessels, where these are present (mammals) tend now to be excluded from the area so as not to interfere with clear perception, and the chorioid may have to thicken locally to carry the extra nutritional load. The increased length of the visual cells has a fortuitous but very fortunate effect upon the burden carried by the mechanism of accommodation (see pp. 30-1).

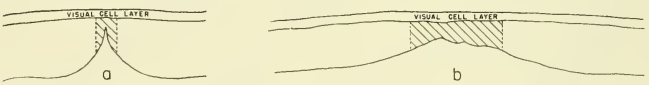

Fig. 75—Well-developed (avian) and poorly-developed (human) foveæ. ×27½.

Cross-hatched in each diagram is the portion of the foveal retina which is actually thinner than the retina *outside* the area centralis. The superior avian fovea is less a 'thin spot' than is that of man. a, foveal region of hawk, *Buteo b. borealis*. b, macular region of normal human retina.

The increase in the percentage of cones results in a great increase in the number of bipolar and ganglion cells, since cones are summated less in them to begin with, and less within the area than outside of it —each cone, ideally, coming to have its own bipolar and ganglion cell transmission-line to the brain.

The thickenings of the visual-cell, outer nuclear, inner nuclear, ganglion-cell, and nerve-fiber layers add up to a local thickening of the retina as a whole. Where this might become extreme, a fovea develops—not to combat the thickening as such, but rather the convex surface thereof which bulges into the vitreous.

The Fovea—The reader, stopping at any point in the above discussion, would then have already read a complete description of some area centralis which actually exists in some vertebrate or other. Most areæ do not go on to develop a fovea, and fewer still of these have produced the

local yellow pigmentation which creates a macula lutea and is a final refinement in making the area centralis the spot of maximal visual acuity. For the full comprehension of the meaning of the foveal depression we must revert for a moment to the elements of physiological optics.

A light ray passing through the cornea and lens and striking the retina perpendicular to its surface will travel on through the retina with its direction unchanged. It was long thought, however, that an appreciable amount of the light would be absorbed and scattered in the retinal tissue before reaching the visual-cell layer, thus not only being lost for purposes of image-formation but, more important by far, tending to blur the image. The depression of the fovea was then thought of as a thin spot produced for the sake of thinning, and serving to remove tissue

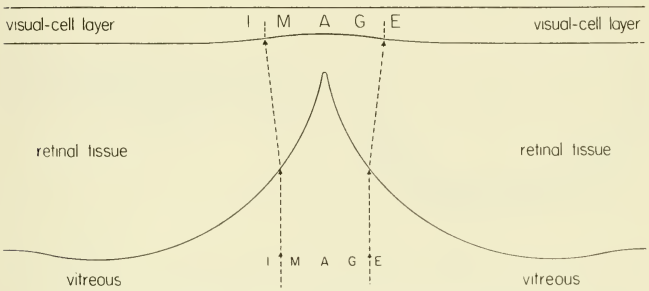

Fig. 76—Local magnifying action of the foveal depression (based on the central fovea of a hawk, *Buteo b. borealis*).

from in front of the important central bouquet of cones in the area. This theory must be discarded however, for in the best of areæ (in lizards and birds) the portion of the depressed retina, which is thinner than the retina outside the area, is smaller than in areæ with shallow foveæ which are known to be degenerate (Fig. 75). The retina, in life, is completely clear and actually extinguishes no more light than the same thickness of vitreous—which, of course, fills in the foveal excavation.

A clue to the real meaning of the fovea (Fig. 76) was made available a half-century ago in some observations of Valentin on the refractive index of retinal tissue; but, it went unrecognized as a clue until very recently. The data never seemed of any possible usefulness, and one finds no figures given in modern reference books. But the index of the retina was

carefully measured by Valentin in a number of animals and was found to be always substantially higher than that of the vitreous. What this means is that if a light ray should strike the vitreoretinal boundary at anything *but* a right angle it will be refracted away from an imaginary perpendicular to the surface at the point of its impact.

The foveal depression is designed deliberately to take advantage of this refraction. The foveal portion of the retinal image is expanded on its way through the retinal tissue, and is thus magnified somewhat when it reaches the level of the visual cells. In birds the magnification is about 13% linearly, 30% in area; and it is probably greater in lizards. The linear increase directly affects visual acuity. The areal increase improves the perception of 'pattern', though it adversely affects sensitivity to external illumination. A part of the lengthening of foveal cones, two advantages of which have already been mentioned, is perhaps in compensation for the local dimming of the expanded portion of the image.

When an area centralis has done everything else possible to increase the number of receptor-units over which the image will fall, the further increase afforded by a deep fovea makes the production of one decidedly worthwhile—nay, mandatory, for the convex bulge in the internal limiting membrane over a highly-developed area centralis would tend to *converge* the rays of light and make the image, at the level of the visual-cell layer, *smaller*. The shallow depression in the area centralis of a soft-shelled turtle (Fig. 78b) or the average teleostean fovea probably does little more than cancel the minifying effect of the area's convex inner surface. The deeper the actual depression goes below the original level of the retina, the higher the mound or 'circumfoveal eminence' created around the depression by the displaced tissue. Since a continuous steep slope is thus produced from the crest of the mound to the bottom of the depression, this sloping surface becomes an effective magnifying device, of optically unique description.

Distribution—No lamprey has an area centralis, but one occurs in *Mustelus*—the only genus of sharks known for certain to have any cones at all. It is marked by a noticeable concentration of ganglion cells (Fig. 77a). An area centralis is very commonly seen in bony fishes, and a fovea (Fig. 77b) has been found in a score or so of teleosts (see Table III, p. 187), never as deep as in lizards but with both rods and twin cones excluded from it. The areæ centrales of frogs, most turtles (Fig. 78), and all crocodilians are devoid of foveæ and are imperfect in that they contain rods as well as cones—indeed, the crocodilian is nocturnal

and it is more than likely that its area centralis is an area of especial *sensitivity,* not of *acuity* at all.*

In only two genera of snakes is a fovea positively known to occur. The East Indian long-nosed tree-snake, *Dryophis mycterizans* (Fig. 79) has a keyhole-shaped pupil with the slot of the keyhole pointing forward well beyond the rim of the lens, thus constituting an extensive aphakic space. The fovea in *Dryophis* is at the outer rim of the retina on the temporal or caudal side of the eye, and a line from it through the center of the lens passes out through the slot in the keyhole pupil, along a groove on the cheek in front of the eye, and straight forward parallel to the axis of the body. It is significant that herpetologists have long

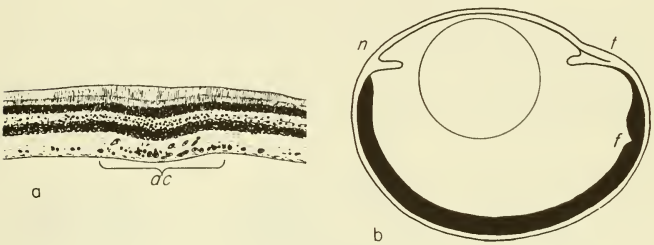

Fig. 77—Area centralis and fovea in fishes.

a, portion of retina from sagittal section of eye of a shark, *Mustelus mustelus.* After Franz. *ac-* area centralis (note increased length and concentration of visual cells, number of ganglion cells).

b, eye of a teleost, *Serranus scriba,* horizontal section; retina shown in black. After Kahmann. *f-* fovea; *n-* nasal side; *t-* temporal side.

*The same suspicion falls upon the ungulates and carnivores, hardly any of which are strictly diurnal. The majority of afoveate areæ would in fact bear re-investigation with this suspicion in mind, for it is already known that the special area of the opossum has its histological peculiarities aimed at increasing sensitivity, not resolving power. There appear to be circumscribed central areas of extreme sensitivity in the retinæ of the echidnas and some 'edentates', for these nocturnal animals are reported to wince and close their eyes in evident distress whenever the light-beam of an ophthalmoscope strikes the small area mentioned.

This, by the way, is quite a different thing from the phenomenon in the human eye which has led some careless ophthalmologists to refer to the macula lutea as the 'most sensitive' spot in the human retina. It is the *least* sensitive spot, becoming quite blind in low illumination—but it happens to be the pupillomotor area, the part of the retina which controls reflexly the closure of the pupil when illumination is suddenly increased. The fovea of the owl is also the pupillomotor area—and here, perhaps, it is extremely sensitive as well, in the true sense of 'sensitive'.

been in agreement that this snake has the sharpest sight and the most accurate judgment of distance of any in the world. A very similar situation obtains in the African bird snake, *Thelotornis kirtlandi;* and probably also in *Dryophiops,* whose pupil is similar.

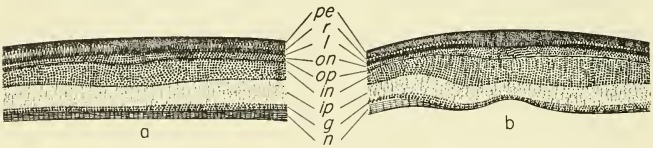

Fig. 78—Area centralis and fovea in turtles. × 60.

a, sagittal section of retina through the area centralis of the western painted turtle, *Chrysemys picta marginata.* The optic nerve head is out of the picture a bit to the right.

b, section of retina through the fovea of a soft-shell turtle, *Amyda* sp. Redrawn from Gillett. *pe-* pigment epithelium; *r-* receptor layer; *l-* limitans; *on-* outer nuclear layer; *op-* outer plexiform layer; *in-* inner nuclear layer; *ip-* inner plexiform layer; *g-* ganglion layer; *n-* nerve fiber layer.

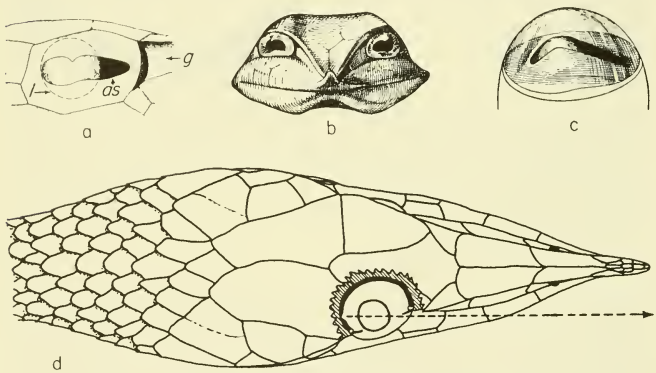

Fig. 79—The East Indian long-nosed tree-snake, *Dryophis mycterizans.*

a, right eye in situ, from the side, showing aphakic portion of pupil and cheek groove which permits straight-forward vision. × 4. From alcoholic specimen. *as-* aphakic space; *l-* lens; *g-* groove. b, face, showing provisions for binocular vision. × 2. From Franz, after Beer. c, anterior segment of right eye, showing form of iris, lens, and aphakic space. × 4. From Franz, after Beer. d, head from above, cut away to reveal eye in section, showing line of sight from temporal fovea through lens and aphakic portion of pupil and along cheek groove. × 2. From alcoholic specimen and microscopic preparations.

TABLE III — AREAE AND FOVEAE

				AREA	FOVEA
FISHES	Cyclostomes				
	Elasmobranchs			*Mustelus* only; central and round	
	Chondrosteans, Holosteans, Dipnoans, Cladistians				
	Teleosts	Many		temporal; poorly defined at best	*Bathytroctes* (deep-sea) has pure-rod fovea
		A few littoral marine spp.		temporal (nearly central in *Hippocampus*)	shallow to medium (deep in *Girella sp.*?)
AMPHIBIANS		Anurans		crescent over optic papilla:	
		Urodeles and Cœcilians			
REPTILES		*Sphenodon*		central	medium (pure-rod!)
		Crocodilians		horizontal band (probably not an acuity area)	
		Turtles		central, round	*Amyda* only; shallow
		Lizards	Nocturnals		
			Diurnals	central; round or oval (temporal in *Varanus*)	deep (shallow in large skinks and *Varanus*)
		Snakes	Nocturnals		
			Diurnals	temporal; poorly defined	*Dryophis, Dryophiops,* and *Thelotornis*; medium
BIRDS	Most (including most vultures?)			central, round	medium to deep
	Some ground-feeders; domesticated spp.			round, poorly defined at best; often absent	pigeons only (shallow and variable)
	Some ground-feeders; many swimmers, divers, and waders			central and round, set in horizontal band which is also organized for acuity	medium, in round area:
	Hawks, eagles, swallows, terns			two circular, foveate areas connected by horizontal band: (terns:)	have visual trident: two: central (deep) & temporal (usually medium, but is the deeper of the two in eagles)
	Kingfishers, bitterns, humming-birds, some wing-feeding passerine spp.			two: central and temporal, both round, not connected by a band	have visual trident: two: central (deep) temporal (medium)
	Some gulls, shear-waters, flamingo			horizontal band	linear (trough-like) fovea
	Owls, *Apus apus, Strigops habroptilus*			temporal, round (a faint central one also in *Apus*)	shallow; sometimes none
MAMMALS		Most			
		Ungulates		more or less temporal; usually broad horizontal band	
		Carnivores (espec. felids)		central, compact	
		Squirrels (espec. marmots)		horizontal band, not well defined	
		Primates	Lower (and *Aotus*)	*Lemur catta, L. macaco,* and *Aotus* only; central	
			Higher	central, round	deep but broad in man (more abrupt in some?)

In lizards the area is central, and is circular or oval; but in birds it is often a long horizontal band, as in Figure 80a (minimizing the need for eye movements) and has in it a central circular or oval fovea. In a number of birds a second fovea, seldom as well-developed as the central one, lies temporally from the latter (Fig. 80b). Such a temporal fovea is comparable with the single fovea of *Dryophis* or a teleost, in that it and its mate in the other eye can both be brought to bear upon the same point in space ahead of the bird. The central or nasal fovea is useful only for monocular vision sidewise from the head; and in most birds, whose eyes aim much more sidewise than forward, it is the only fovea. In the owls, only a fovea temporalis is ever present, and it may be very

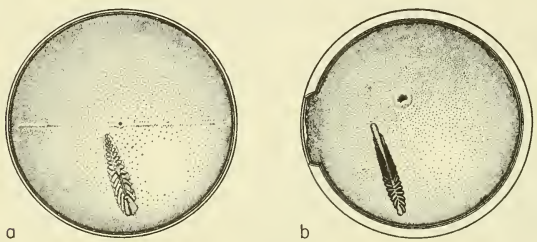

Fig. 80—Ophthalmoscopic appearance of bird eyes, showing pecten (ventrally), areæ, and foveæ. After Wood.

a, right eye of pigeon guillemot, *Cepphus columba,* showing horizontal linear area centralis and single central fovea. × 3. b, right eye of Anna's hummingbird, *Calypte annæ,* showing central foveate area, and temporal fovea (in cutaway; *cf.* Figs. 114-5, pp. 308-9). × 10.

shallow or even lacking. One swift, *Apus apus,* approaches the owls in that its central fovea is barely visible though the temporal one is well developed. Only birds ever have two foveæ per eye, but George Moore has recently found that some of the killifishes (*Fundulus* spp.) have two horizontal, ventro-temporal, ridge-like areæ.

In diurnal birds and in most lizards, excepting the monitors and the more chunky and sluggish of the skinks, the fovea is deep and its slope ('clivus') is convex. This convexiclivate type of fovea (Fig. 81) occurs only in the very best-constructed of areæ centrales. The less perfect areæ of fishes, *Sphenodon,* owls, domestic birds, and man all have shallow and concave ('concaviclivate') foveæ (Figs. 75b, 82). It is safe to say that most of these (the fishes excepted) are degenerate and formerly,

in some ancestor, tended more toward the convexiclivate type of profile. The visual cells of *Sphenodon* show that this animal was once diurnal (see Chapter 16, section C) and at that time it no doubt had a fovea

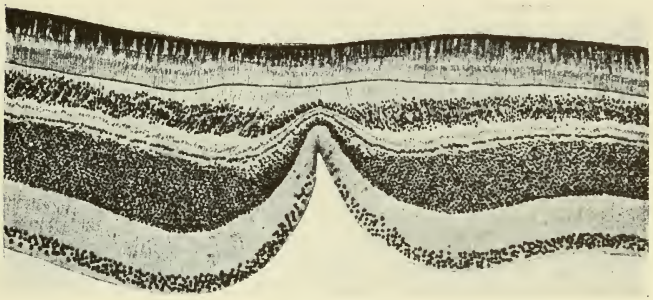

Fig. 81—Central (nasal) fovea of the European bank swallow.

Exemplifying the deep, convexiclivate type characteristic of birds and lizards. After Rochon-Duvigneaud.

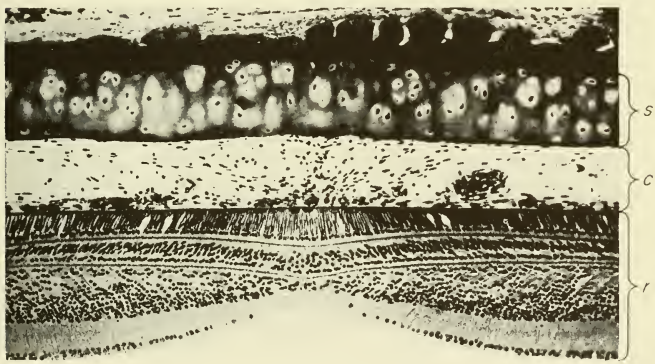

Fig. 82—Fovea and surroundings in *Sphenodon*. ×90.

Illustrating the shallow, concaviclivate type characteristic of fishes and of those vertebrates whose foveæ have become degraded through domestication or the abandonment of strict diurnality. *s*, sclera; *c*, chorioid; *r*, retina. (The retinal and chorioidal pigment have been bleached from the section; note that only rods are present—this is the only rod fovea in a terrestrial vertebrate).

as acutely deep as that of any lizard. Its pure-rod retina was once a pure-cone one, so that *Sphenodon,* having retained the fovea despite the transmutation of its cones into rods, now enjoys the only pure-rod fovea which is known to us, except for the very mysterious case of a reputed fovea in one deep-sea fish *(Bathytroctes).* Similarly, the foveæ were certainly much better developed in some of the owls' diurnal ancestors. The shallowness and variability of the pigeon's fovea has long been considered the consequence of semi-domestication, for in the fully domesticated fowls the fovea is gone completely. On the other hand, the concaviclivate foveæ of the few foveate teleosts, and that of the only known foveate turtle *(Amyda)* have probably never been any deeper—they seem merely intended to counteract the convexity of the area centralis. And, by the way, some pure-cone animals with extremely good vision—the ground-squirrels, particularly—have never produced a fovea simply because their entire retina is built as well for acuity as is the macula of man.

If the variable, shallow, and gradually-curved human fovea has not degenerated from a deeper and much more abrupt depression, it is difficult to see what could have called it into being. Its magnifying action on the image is probably negligible compared with that of a convexiclivate fovea. Nothing much seems to be known as to the shape of the foveal depression in some of the monkeys and apes which are more strongly diurnal than man himself. In the marmoset (*Hapale jacchus*) however, the fovea has a very steep clivus and a small flat floor. The sooty mangabey (*Cercocebus torquatus*) probably has the most cone-rich retina of any primate, and its foveal cones are the longest and slenderest in mammals; but the shape of its fovea is unfortunately in dispute. One or two divisions of mankind—the Hottentots, certain natives of India, and the Tierra del Fuegans—are known to have phenomenal visual acuity; but the profiles of their foveæ are not accurately known. Their sharpness of sight has always been attributed to an unusual slenderness of the foveal cones.

The distribution of areæ and foveæ, and particularly their topographical locations in various retinæ, are discussed further in section C of Chapter 10. As we have seen, the modifications themselves are devoted entirely to the raising of local visual acuity, but their locations are of such importance in connection with eye movements and space-perception that their full significance can be gathered only from a later consideration of these matters.

(D) Intra-Ocular Color-Filters

Color vision itself is a potent aid to visual acuity in its broad sense, and was certainly evolved for this application rather than for the æsthetic ones which it has come to have in human vision. But color vision is such a large topic, with so many ramifications, that it needs a long section to itself (Chapter 12). In the present section, we shall consider a group of devices which occur only in the eyes of diurnal animals (some, not all, of which have color vision) and promote their visual acuity, and which look at first glance as though they must have something to do with creating color vision—though actually they are just as effective whether their owners happen to be able to distinguish hues or not.

Types and Distribution—The yellow pigmentation of the human area centralis—making it a macula lutea—was discovered by Soemmering in 1818. In 1840, Hannover first described the oil-droplets which are characteristic of so many vertebrate cones (Fig. 22, p. 54). Some or all of these are always yellow, when any pigment is present in them at all. By 1867, Max Schultze had called attention to the fact that the rich network of capillaries in the inner layers of the mammalian retina constitutes an effective yellow screen through which the visual cells must look. In 1887 Schiefferdecker found that in certain fishes the cornea is yellow. (Soemmering, long years before, had seen the color in the pike, but thought it to be in the aqueous humor). Other species have recently been added to Schiefferdecker's list, and in the past few years it has been found that diurnal squirrels, tree-shrews, snakes, geckoes, and lampreys (except *Geotria*) have yellow lenses. It has been known for many years that the adult human lens is yellow, but not until very recently has it transpired that this is actually of advantage to sharp vision in bright light.

This imposing list of intra-ocular color-filters exhibits at first glance considerable variety; but (see Table IV, pp. 200-1) they are almost all yellow; and where they are not, they are still of long-wave colors—and they are confined to diurnal vertebrates. It thus appears logical that some inclusive interpretation may hold for all of them, and after a large number of false starts such an interpretation has finally been given. But until a few years ago the macular pigment, retinal capillaries, and yellow corneæ were neglected or forgotten, and the yellow lenses went undiscovered for a most surprisingly long time, while attention was fastened upon the

colored oil-droplets. As long as these held the stage, the mental myopia of investigators prevented anyone's noticing the other types of filters and using them to help explain the baffling oil-droplets.

The Color-Vision Theory—The oil-droplets were formerly believed to occur in a much greater variety of colors than is actually ever the case. Those of birds seemingly ran the gamut of the visible spectrum; but under modern apochromatic microscope lenses the violet, blue, and green droplets lose their colors and are seen to be actually devoid of pigment. They owe their chromatic appearance, under cruder lenses, to purely optical phenomena. Only red, orange, and yellow droplets occur in birds and turtles along with some colorless droplets. Most groups provided with colored droplets contain nocturnal species whose droplets are all colorless. The pigments involved are carotenoids, and those extractible from chicken retinæ have recently been tentatively identified as astacin, sarcinene, and xanthophyll.

When belief was current in a more complete spectral representation, the theory of oil-droplet function first advanced by Krause in 1863 (and based at first upon the supposition that lizards, as well as birds, had 'all' colors) was most popular, and still has adherents. According to this theory, each color of oil-droplet makes possible the independent sensation of the corresponding color in the spectrum. The supposition was that the bird has but one (not three) photochemical substances in its cone outer segments (see p. 91), and that this undifferentiated substance would be affected equally by any and all visible wavelengths of light. Discrimination of wavelengths on a qualitative basis—color vision, in other words—would be possible only if certain cones were allowed to be stimulated only by certain wavelengths, others by other wavelengths, and so on. The differently colored oil-droplets, standing in the pathway of the light on its course toward the percipient outer segments, were supposed to ensure this differential stimulation of different sets of cones, which in turn connected with different sets of brain cells in which the respective color sensations were registered. This mechanism of color vision has seemed so simple and plausible that some students of human visual physiology have fled to it as a refuge from the necessity of thinking through the state of affairs where, as in man, color-vision occurs with all the cones alike, and have postulated that minute colored oil-droplets occur in human cones—the while being careful not to look to see if they are really there.

The ingenious color-vision theory of oil-droplet function falls to earth under several blows: the number of oil-droplet colors does not in fact correspond to the range of the bird's spectrum, which is now known to be co-extensive or even a little wider than our own. Lizards have a complete color-vision system, yet have only yellow oil-droplets. There are vertebrates far below the birds—the fishes—that have color vision without benefit of oil-droplets, which could then scarcely be considered a primitive device for hue-discrimination. Most important of all, it has been known (though almost forgotten) for decades that the cones of the bird fovea contain only yellow droplets, the red ones stopping at the margin of that all-important retinal pit. This demonstrates not only how wholly illogical it is to suppose that the bird would be able to perceive only *yellow* in the fovea, and all other colors only outside it, but also that the different colors of droplets are of unequal importance and have different uses, not one common function. The exclusively yellow droplets in the avian fovea line up with the yellow filters, whether composed of oil-droplets or not, of all other vertebrates. Yellow droplets appeared first in evolution, in lower vertebrates; and where the oil-droplets are decadent, as in nocturnal birds, some yellow ones may persist but no red ones ever occur. The red filters of birds and turtles can be temporarily ignored while we consider what the much more common yellow filter may do for photopic vision.

Yellow Filters and Chromatic Aberration—The image formed by the natural dioptric system of the eye does not lie in a single plane or spherical surface, even when the object is a plane or a curved surface concentric with the eye. The image has *thickness,* owing to aberration which is of two kinds, spherical and chromatic. Spherical aberration results from the failure of the cornea and lens to bring parallel rays to a single point, and since it is chiefly caused by the improperly curved peripheral portions of the corneal and lens surfaces, it is effectively combatted by the pupil which acts as a 'stop'. When the refractive power of the lens is increased in accommodation, the pupillary aperture automatically contracts to afford the smaller stop which is then demanded.

Chromatic aberration is due to the fact that the different wavelengths of white light are not all bent to the same extent when they are refracted at boundary surfaces. The refractive index of a substance is thus different for each wavelength—it is this phenomenon of 'dispersion' which makes it possible for a prism to form a spectrum by sorting the 'colors'

out of 'white' light. The shorter waves are bent most, longer waves progressively less. As Figure 29c (p. 82) shows, this results in a series of focal points beyond a lens, the violet focus being nearest and the red focus farthest away. The distance occupied by these foci is called the linear chromatic aberration, and in the human eye it is considerably more than the whole thickness of the retina. In the refractionist's language, the aberration amounts to about two diopters. The 'normal' or

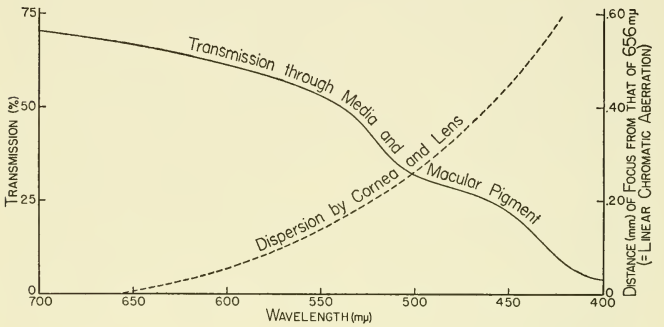

Fig. 83—Graph showing how yellow filters combat chromatic aberration.

(Curve of transmission spectrum smoothed from data of Ludvigh and McCarthy on absorption in the lens, cornea, and humors of the human eye, integrated with data of M. Sachs on absorption in the most completely studied macula among his nine examples; dispersion curve for the human dioptric media, showing the relative refrangibility of the various wavelengths, plotted from data of Polack).

The curves bring out the fact that the short waves, which are most strongly dispersed and which consequently contribute most to chromatic aberration (*cf.* Fig. 29e, p. 82), are the ones most strongly absorbed (*i.e.,* least well transmitted) by the yellow filters interposed in their path within the eye.

emmetropic human eye is actually emmetropic only for yellow light, and is, simultaneously, 0.75 diopters hypermetropic for red and 1.25 diopters myopic for violet. Since the dioptric apparatus ordinarily places the yellow focus in the visual-cell layer, we must actually *accommodate* when diverting our attention from a blue object to a red one at the same actual distance from the eye, and must relax accommodation upon looking back at the blue object. This fact is employed by astute artists to heighten the illusion of depth in their paintings.

If a particular color-focus lies squarely in the visual-cell layer, the homonomous color-value of the external visual field will be crisply focused but all others will be represented, at the level of the visual cells, by sets of blur-circles. Fortunately the ends of the spectrum are much less bright than the yellow region; but even so, chromatic aberration results in a considerable blurring of the image.

In the fovea, chromatic aberration is partly compensated for (except in birds), by the greater length of the foveal cones (how many things we find we can do with that greater length!), for a greater number of color-foci can thus lie in the length of one cone. But foveal cones have their limits in length, and fall far short of dealing adequately with chromatic aberration by such means. Obviously, there would be no chromatic aberration if a single wavelength of light were passing through the eye to the receptor layer. To bring this about, however, would mean the elimination of color vision—and of nearly all the light. A compromise must, then, be made by which the spectrum is narrowed down enough to make a big dent in chromatic aberration, without sacrificing much of the physiologically effective energy of whole sunlight, or many of the colors which occur most commonly in nature.

A yellow filter serves this purpose admirably. It cuts out much of the violet light and some of the blue, which are the colors responsible for most of the chromatic aberration, as Figure 83 demonstrates. At the same time it lets through, unimpeded, most of nature's hues, and passes the spectral regions which look brightest to both light- and dark-adapted eyes.

Other Values—This reduction of the effects of chromatic aberration is not the only performance of a yellow filter. Most scattered light is of short wavelengths, and under bright-light conditions this scattered light results in glare. Glare and dazzle are minimized by a yellow filter. Similarly, the unfocusable shortwave light scattered in the atmosphere, and responsible for the bluish cast of distant mountains and for the blue of the sky, is cut out by a yellow filter which, as every photographer knows, creates a sharper image.

Still another effect is the enhancement of contrast. It will be recalled that the same color-sensation can be aroused by different mixtures of wavelengths. One can easily find, say, two books on the shelf whose colors appear to be identical blues or greens. Yet a spectral analysis of the light reflected from them might show the like-seeming colors to be wholly different in wavelength composition. Almost any filter of colored glass or

gelatine, placed before the eye, will make the two books look unlike; for certain wavelengths reflected by the pigment of one, and absorbed by the filter so as to change the color seen through the latter, are not necessarily emanating from the other pigment at all. By absorbing wavelengths common to the two unlike mixtures, the filter brings out the fact that they *are* unlike, which is something the unaided eye cannot detect.

A filter thus produces contrast between colored areas which otherwise would look alike and would therefore be without a discernible boundary between them. This fact was put to important use in World War I, when colored goggles worn by reconnaissance aviators enabled them to detect green camouflage produced by paints whose reflection-spectra were not at all like those of the chlorophylls of actual foliage. Modern 'foliage' camouflaging is more troublesome to both adversaries, for it has to consist of actual foliage, which must be replaced frequently as it fades.

A filter naturally tends to abolish just as many contrasts as it promotes; but promotion is in advance of abolition when yellow filters and natural colors are under consideration. By cutting out the different amounts of blue in different but alike-looking green mixtures, the greens are made to look unlike; and almost any other contrasts can be sacrificed by the animal if only those between *greens, so* numerous in nature, can be enhanced. The oil-droplet type of filter has a special advantage, since the many colorless or other-colored droplets scattered among the yellow ones in the whole mosaic will permit the perception of any contrasts which the yellow droplets tend to iron out, and vice versa. By altering the proportions of the different colors of droplets in different parts of the retina, particular color-contrasts are enhanced in particular parts of the visual field. Thus in the pigeon the ventronasal three-quarters of the retina have the yellow droplets predominant, giving maximal contrast of objects seen against the sky by eliminating the latter's blue color; while the dorsotemporal quadrant, being especially rich in red droplets, affords maximal visibility to objects seen against the green of the fields and trees over which the bird is flying. In World War II, antiaircraft observers have stumbled onto such tricks, and have learned to use filters when scanning the sky for enemy planes.

One thing which yellow filters might do—but don't—would be to absorb harmful ultra-violet rays before these could reach the delicate cone outer segments. Experiments have shown, however, that none of these rays survive absorption in the cornea and lens of a pigeon's eye, whose oil-droplets consequently cannot possibly be purposed to protect against them.

Red Filters and the Rayleigh Effect—A very widespread superstition, showing itself in such things as red airport beacons and amber foglights on automobiles, is the notion that some colors—notably red—penetrate fog better than do other colors or white light. The supposed phenomenon is attributed to the 'Rayleigh effect', which is the scattering of light inversely as the fourth power of the wavelength. The short waves are scattered the most, the red and infra-red ones scarcely at all, resulting in the blue coloration of the sky and in the remarkable clear pictures which can be taken through haze with infra-red-sensitive plates.

But as far as the visible spectrum is concerned, there is no Rayleigh scattering at all when the particles which cause the scattering are larger in diameter than 0.75μ. Natural mist and fog droplets, and solid particles suspended in natural waters, are invariably at least several times this size, and scatter light quite irrespective of wavelength. Red oil-droplets cannot, then, be designed to sharpen images by eliminating Rayleigh-scattered light in misty weather or in water, as some have thought. The turtles and birds have nothing in common, and if this inclusive explanation will not hold for the red oil-droplets of the two groups, room is left for independent explanations of the two cases.

Value of Red Oil-Droplets in Birds—Most birds are such early risers that they expose themselves to Rayleigh scattering—not by gross mist particles, but by molecules of water and gases in the atmosphere of even the clearest of sunrises. At this time of day the sun's rays slant through such a long atmospheric pathway that they appear reddened, the same being true of the sunset—which is more familiar to most of us. The bird, getting in most of his day's work at dawn and shortly after, is aided by his red droplets. As the day wears on and the sunlight whitens, the yellow (and on dull days, the colorless) droplets take over—the orange ones affording a smooth transition. If this explanation is true, one would expect late-rising birds to have few red droplets. This is indeed the case, for whereas the song-birds average 20% red droplets, the hawks have but half of this number; and in the crepuscular swifts and swallows there are but 3% to 5% red droplets.

Value of Red Oil-Droplets in Turtles—The significance of the red droplets of turtles is rather different. More than any other diurnal vertebrates, they have the problem of seeing over the glary surface of water. Since they have intensity to spare, they can afford red droplets for the even greater effect upon chromatic aberration which a red filter will have,

as compared with a compromise yellow one. On less bright days, the turtle's yellow, or even his colorless, droplets automatically replace the red ones as the most important constituents of the whole mosiac. Thus the birds and turtles, having sufficiently cone-rich retinæ, have been able to differentiate the cones into several populations. Where most retinæ are rod-and-cone, or duplex, the turtles and birds have produced what may fairly be called *multiplex* vision.

The workings of the turtle's oil-droplet mosaic can best be gathered from an account of a clumsy, man-made imitation worked out empirically by the United States Navy, as described to the author by Mr. Laurence Radford of the Bureau of Ordnance:

"The Navy uses both red and yellow color filters in optical instruments. Both are made of Corning Glass. The red cuts quite sharply at about λ6000-6200 [Å.u.] and the yellow at about λ5100-5300 [Å.u.]. These filters are used because much experience has shown that they are helpful, and the particular filters selected were chosen after considerable study, both experimental and theoretical.

"In my opinion these filters are effective for our purposes because they reduce glare due to scattered light and minimize the effects of the chromatic aberration of the eye, and for these reasons almost exclusively. These two effects are produced more intensively by red than by yellow filters, *i. e.*, the amount of scattered light transmitted by the red is much less than by the yellow because the latter transmits the green; and with the red filter the effect of chromatic aberration is practically eliminated. But there are conditions when the red filter cannot be used effectively, perhaps because of insufficient intensity of illumination, or perhaps because it would reduce the color contrast. Hence the two colors, giving us essentially the choice of two degrees of the same effect."

The red and yellow oil-droplets of the domestic hen have been found to cut the spectrum off respectively at λ5800-5900 Å.u. and λ5150-5250 Å.u., the extracted red pigment (astacin) and yellow pigment (xanthophyll) at λ5900 Å.u. and λ5200 Å.u. respectively when dissolved in castor oil. Perhaps when the droplets of turtles are studied more carefully they will be found to come even closer to justifying the Navy's choices!

In this connection it is significant that the kingfisher, whose visual problem, like that of the turtle, is complicated by glary water, has 60% red droplets—three times as many as the average bird. So much for the functions of the intra-ocular color-filters. Some remarks on their nature and evolution are now in order.

Phylogeny and Chemistry of the Intra-Ocular Filters—The oldest of all appears to be the yellow lens, which occurs in lampreys (but not in the nocturnal *Geotria*). Here, as well as in snakes and squirrels, the pigment involved (lentiflavin) is soluble in weak alkalies. It is present in full amount in albino squirrels, hence cannot be scattered melanin, but is a chemically distinct substance (consult Table IV, next page).

In at least one of the two or three diurnal geckoes (*Lygodactylus*), and in the strongly diurnal, squirrel-like tree-shrews (*Tupaia*) the lens is also yellow though nothing is as yet known about the pigment itself. Presumably it is lentiflavin which, since it has been evolved repeatedly in such widely-scattered groups, probably has as its precursor some substance which is present in all vertebrate lenses.

The most intense colorations of the lens are reached in the ground-squirrels and prairie-dogs, where the lens is almost orange. The lenses of all other American sciurids (excepting the pale ones of the gray squirrel and the colorless ones of the flying squirrels) are alike in color and are matched by a 2 mm. thickness of American Optical Company 'Noviol 0' glass. 'Noviol 0' is matched by the lens of *Malpolon monspessulanis,* regarded as the most sharp-sighted snake in Europe, and will probably be found to be exceeded in coloration by the lenses of *Dryophis* and its relatives. Other diurnal snakes have paler lenses, the coloration being deepest in swift, bright-light species such as the racers and whipsnakes. Crepuscular snakes have little lentiflavin, nocturnal species none at all. Lamprey, *Lygodactylus,* and *Tupaia* lenses compare with those of a gray squirrel or a whipsnake.

The yellow coloration of the human lens is the result of a precocious aging of the lens nucleus which commences actually before birth, and is thus not on the same footing as that of other yellow lenses. It grows steadily in depth throughout life—the lens of a child has been found to absorb 10% of the blue light entering the eye, that of a 78-year-old man 85%. In the normal adult human eye, absorption in the dioptric media increases gradually from the long-wave to the short-wave end of the spectrum, attaining a value of over 90% in the violet. In old age the spectrum is cut off in the blue-green region and aged artists find that their blue-containing pigment mixtures look wrong to younger persons, unless the painting is done under an illumination which is particularly rich in short-wave light, such as that from a mercury vapor lamp. The pigment is melanin formed by the interaction of protamine and cysteine liberated by protein-breakdown. The development of the coloration is thus due to

TABLE IV — INTRA-OCULAR COLOR-FILTERS

					HABITS AS TO LIGHT	OIL-DROPLETS IN CONES	YELLOW LENS	YELLOW CORNEA	MACULA LUTEA	RETINAL CAPILLARIES
FISHES	Cyclostomes	Hagfishes			blind					
		Lampreys	Petromyzontidae		diurnal		+			
			Geotriidae		nocturnal					
	Elasmobranchs				nocturnal or benthic; some bask					
	Chondrosteans				benthic	colorless				
	Holosteans				diurnal	lost		+ in *Amia*		
	Dipnoans and Cladistians				nocturnal	colorless where any				
	Teleosts	*Esox* et al			strongly diurnal	lost		+		
		Others			various			+ in a few (e.g. *Cyprinus*)		+ eels only
AMPHIBIANS		Anurans	Frogs		arhythmic	yellow and colorless				
			Toads, Hylas		nocturnal	(have been lost)				
		Urodeles and Cœcilians			secretive, fossorial					
TILES	*Sphenodon*				nocturnal, fossorial	pale yellow				
	Crocodilians				nocturnal	(lost)				
	Turtles				diurnal	red, orange, yellow, colorless				
	Lizards	Most			diurnal	yellow and colorless			in chameleons?	
		Worm-lizards (four families)			fossorial	colorless				
		Helodermatidae and Xantusiidae			nocturnal	colorless				
		Pygopodidae			nocturnal	(lost)				

REP	Lizards	Geckoes	Most (including eublepharids and *Uroplatus*)	nocturnal	(lost)				
			Several genera	diurnal		+(*Lygodactylus*, at least)			
	Snakes	Most colubrids and elapids		diurnal	(lost by fossorial ancestor)	+			
		Some colubrids; illysiids, uropeltids, *Xenopeltis*		crepuscular or secretive		+(pale to colorless)			
		Many colubrids; some elapids; boids, chunk-heads, vipers, worm-snakes		nocturnal or fossorial					
BIRDS			Most	strongly diurnal	red, orange, yellow, colorless				
			Many	crepuscular or nocturnal	some yellow, most colorless				
			Some owls (and *Apteryx*, *Strigops*, *Steatornis*, etc.)	strongly nocturnal	colorless				
MAMMALS	Monotremes		*Ornithorhynchus*	secretive, largely nocturnal	colorless				
			Tachyglossus		(lost)				
	Marsupials		Most	nocturnal	colorless				+ in some (out to limitans in *Didelphis*)
			Macropodidae	arhythmic					
	Placentals	Most		crepuscular or nocturnal	(discarded by original nocturnal placental mammals)				+ in most (lacking in, e.g., *Rhinoceros*)
		Ungulates and large Carnivores		arhythmic					
		Insectivores	Most	nocturnal					+
			Tupaia	diurnal		+			
		Rodents and Lagomorphs	Most	nocturnal					+(out to limitans in *Glaucomys*, *Glis*, & *Eliomys*)
			Ochotona, *Castor*	diurnal					
			Sciuridae: Most	diurnal		+			
			Sciuridae: Flying squirrels	nocturnal					
		Primates	Prosimians (and *Aotus*)	nocturnal, except *Lemur* et al					+
			Simians (except *Aotus*)	all diurnal		+(man, at least)		+	

an essentially senescent change, and its optical usefulness is the sheerest of accidents.

Oil-droplets and yellow corneæ both appear first in the chondrostean and holostean fishes respectively. The oil-droplets of the sturgeon are colorless, though they were not necessarily always so. They have been used as an argument that the oil-droplet was first evolved as a colorless focusing device; but the sturgeon has a nocturnally-adapted eye, and one would expect its oil-droplets to be colorless even if they had been pigmented in some diurnal ancestor.

In the diurnal *Amia,* the whole cornea is yellow, with the color intensified dorsally. The pigment itself has not been studied, but it is probably the same ichthyocarotin which occurs in many of the dermal chromatophores of fishes generally. Some teleosts, notably the markedly diurnal pikes (*Esox* spp.) have as strongly yellowed corneæ as *Amia.* In a species of darter from Georgia, so new to science that as yet it has no name, Hubbs reports a central, homogeneous, deep yellow coloration in the cornea, opposite to and co-extensive with the pupil. Other teleosts have various, usually diffuse and pallid yellow colorations; but in most species the cornea is quite colorless. However much a fish may prefer bright sunlight, that light is dimmer through water than it would be on land. No fish can see more than a few rods at best owing to the extinction of light in water, hence few can afford the luxury of a yellow filter unless they are content to use their eyes mostly near the surface. Most fishes enter deep, dim water at some time of the year. They must also do without vision when beneath a covering of ice and snow. The eels are exceptional, below the mammals, in having retinal capillaries; but these are not intended as a filter—their significance is a very special one (see pp. 405-6).

Of the amphibians, only the frogs approach diurnality, and these have oil-droplets which may be colorless, or yellowed by the same carotenoid pigment which colors the animal's fat. Other amphibians lack even colorless droplets.

Among the reptiles *Sphenodon* is at once conspicuous since, though nocturnal, and with its visual cells almost all converted from cones into massive rods (see Chapter 16, section C), the oil-droplets and some yellow pigmentation thereof have been retained. The reader will remember that *Sphenodon* has also kept the fovea of its diurnal forebears. (Fig. 82, p. 189). The turtles have ruby-red, orange, and lemon-yellow oil-droplets. The crocodilians, like the similarly nocturnal toads, have got-

ten rid of all droplets. So have many lizards and the snakes; and it is in these two groups that we find evidence that once the oil-droplets have been lost, they can never be regained:

Most lizards are diurnal and have bright yellow and colorless oil-droplets. In the chameleons, there is claimed to be an additional yellow pigmentation of the inner layers of the retina in the region of the fovea, though this matter requires further investigation. Secretive and fossorial lizards such as *Anniella* have lost most of the pigment of the oil-droplets, and nocturnal above-ground forms like *Xantusia* and *Heloderma* have only completely colorless droplets. The logical final step has been taken by the geckoes, which probably passed through a *Xantusia*-like stage (consult Fig. 25, p. 62) but later eliminated the useless, colorless oil-droplet entirely. Some geckoes are so small, with such tiny eyes (*e. g., Sphærodactylus* and *Gonatodes* spp.), that they are able to be more or less diurnal without benefit of a slit pupil. A couple of genera of good-sized geckoes (*Phelsuma* and *Lygodactylus*) are round-pupilled and diurnal, and have eyes large enough to demand special provisions for this habit. It is probable that in them the visual cells have been reconverted into cones, and in *Lygodactylus* at least the lens is known to be yellow.

The bearing of the structure of the eye upon the problem of the origin of the snakes will be discussed later (Chapter 16, section D); suffice it to say here that their lack of oil-droplets shows them to have originated as light-shunning forms. The yellow lens has appeared here (as in *Lygodactylus* and the squirrels) because the oil-droplets could not reappear, upon the adoption of diurnality by forms whose photophobic ancestors had discarded them. It is safe to say that any group which has oil-droplets has had unbroken ancestry in forms similarly provided. Thus, the presence of yellow droplets in frogs indicates that the early amphibians, the Stegocephali, had droplets and were diurnal—as indeed we should surmise from their bulk, their consequent need of the warmth of the sun, and their complete freedom from terrestrial enemies during their evolution from the fishes. A similar argument would attribute diurnality to the dinosaurian ancestors of the birds.

Of the mammals, the monotremes are usually called nocturnal though the duck-bill is not strictly so, and has oil-droplets whose color or lack of it has not been ascertained. Droplets occur in marsupials but are always colorless so far as is known, though once erroneously reported to be pigmented in kangaroos. The placental mammals are nearly all crepuscular

or nocturnal, with twenty-four-hour eyes among the ungulates and carnivores. None of these have filters. Only a few placental mammals, mostly squirrels or primates, are strongly diurnal. The yellow lenses of tree-shrews and squirrels, like those of diurnal geckoes and snakes, are to be looked upon as substitutes for the irretrievable oil-droplets of remote diurnal ancestors, which had been discarded by more immediate nocturnal ancestors.

The retinal capillary supply likewise makes its first appearance (except for the eels) among the mammals, and cannot be ignored as a yellow-filtering device. However, it is the least effective of all such devices, for the capillaries are in general no less abundant in nocturnal mammals than in diurnal ones, indicating that they absorb so little light that they do not interfere with scotopic vision. Again, in areæ centrales the capillary network is not richer but is actually diminished, as though the shadows of the vessels caused damage to the image which was not compensated for by any differential filtering action. In the few mammalian areæ which have foveal depressions the capillaries are eliminated entirely. It is in such areæ (in the primates) that we find yellow pigment in the inner layers of the retina—filling in, as it were, the lacuna in the capillary plexus, but far more efficient as a filter than any equal area of the capillary screen.

The nature of this pigment in the macula lutea is unknown. No studies have been made of its status in sub-human primates. The amount is known to vary greatly in different human individuals—being sometimes so great as to render the person wholly blind to blue. Old observations, now considered questionable, seemed to demonstrate more of the pigment in brown-eyed than in blue-eyed persons. It has been claimed to be soluble in alcohol and to change color in acids and alkalies. No modern biochemist has given any attention to the pigment or to a resolution of these apparent ambiguities of genetic and chemical behavior; but a fair guess is that the substance belongs to the carotenoid family of pigments and may be subject to the influence of diet. Simple experiments on the perceptibility of blue stimuli would show whether the macular pigment can be increased by feeding carotene or related substances to human subjects; but such experiments have yet to be made.

The effectiveness, in human vision, of the combination of macular pigment and the yellow lens is difficult to evaluate. We do know that for a few weeks after a person has had cataracts removed, white light looks decidedly bluish to him. We can only guess how much less sharply

we would see without our filters, by determining how much *more* sharply we see with additional yellow filters placed outside the eye. The fact that we can gain appreciably in visual acuity by that means—as any expert rifleman knows—shows, by analogy with the squirrel species of various brightness-preferences, that the human eye is not purposed for use in the very brightest of light. The prairie-dog, which prefers such light, has his intra-ocular filter already so deeply colored that any extra-ocular supplement to it would probably take more away from his vision than it conferred. We are also led to consider man as not inherently strictly diurnal by the fact that the ground-squirrel, the bird, or the diurnal reptile unblinkingly tolerates intensities which force us to screw up our eyelids or run for a pair of dark goggles.

Chapter 9

ADAPTATIONS TO NOCTURNAL ACTIVITY

(A) Nocturnality and the Eye

Nocturnality and Crude Vision—The support of nocturnality, in animals whose eyes mean much to them, comes wholly from great sensitivity to light. This is possible only with a preponderance of rods in the retina, which in turn makes for low visual acuity. However, if a nocturnal animal emphasizes rhodopsin and the length of his rods rather than their diameters, and keeps summation in optic nerve fibers at a minimum, he may be able to retain good resolving power in bright light —provided he has means of reducing greatly the sensitivity of the eye under those conditions. Such means, as we shall see, are exemplified by the common slit-shaped pupil and the rare occlusible version of the 'tapetum lucidum'; and the geckoes show what can be done to make an extremely sensitive eye very valuable in the daytime even to an essentially nocturnal animal, if that animal insists upon being able to come out by day with safety.

Nocturnal adaptation of the eye need not, therefore, be as restrictive as bright-light adaptation. No cone-rich or pure-cone eye is useful at night, but a pure-rod eye may be quite useful by day. But it is only among the geckoes, in *Sphenodon,* and perhaps in the owls that forms having great sensitivity have been able to combine with it a respectable degree of resolving power. By and large, ocular adaptations for sensitivity demand such a sacrifice of visual acuity that they make nocturnal animals largely dependent upon senses other than vision.

The nocturnal animal is primarily an ear- and nose-animal; and this is particularly true of aquatic forms, to which the chemical and auditory senses are especially important because of their enhanced value over distances in water. Both audition and olfaction are promoted under nocturnal conditions, though not because of anything the nocturnal animal has done to modify the receptors of those senses. Odors and sounds are carried better by the night air and are dispelled more slowly because of the absence of rising air-currents. At night, too, sounds have an augmented attention-value since they are of fewer kinds and are out of competition with abundant visual stimuli.

The diurnal animal, because he is cone-rich, has an acuity of vision which makes the eye his best sensory instrument; but the nocturnal form, being cone-poor, has unsharp vision and can make more accurate identifications of enemies and food with his nose than with his eyes. The '*minimum separabile*' for parallel lines—the angular distance they must be apart to be seen as separate—has been determined experimentally for a number of animals by various investigators. Some of the values obtained, not necessarily at all close to maximal and minimal values for all vertebrates, are listed in Table V.

TABLE V

VISUAL ACUITIES FOR PARALLEL LINES (From various sources)

Diurnal animals:	Visual angle, minutes	Corresponding distance on retina, micra	Visual angle corresponding to 1mm. distance along visual cortex
Human adult	0.44	1.89	.....
	0.48	2.06	.....
	0.50	2.14	.....
(different reports)	0.80	3.43	.....
	0.82	3.52	.....
	0.83	3.56	.....
Child	0.62	2.67	.....
Chimpanzee	0.47	1.86	.....
Rhesus monkey	0.67	2.33	.....
Rhesus monkey, along visual axis	.....	.....	4′
Rhesus monkey, 7° from visual axis	.....	.....	20′
Cebus monkey	0.95	3.31	.....
Pigeon	2.70	4.89	.....
Pigeon, 'homer'	0.38	.69	.....
Gamecock (no fovea)	4.07	9.58	.....
Nocturnal animals:			
Cat, along visual axis	5.5	.....	1°
Cat, 30° below axis	.....	.....	5°
Alligator	11.0	.....	.....
Opossum	11.0	.....	.....
Rat, pigmented	26.0	23.8	.....
Rat, albino	52.0	47.7	.....

Advantages and Limitations—It may be stated categorically that nocturnality, wherever it is characteristic of a large taxomic group, has always been adopted secondarily by the ancestral form of the group. Even more certainly, any nocturnal member of an otherwise diurnal group has become nocturnal independently. We can be sure that all vertebrate species would be diurnal if they could 'get away with it'.

The original chordates were bright-light animals. The early fishes invented rods in order to extend their day and to be able to venture from the surface to depths where they were safer, but where the lessened illumination made necessary greater ocular sensitivity. The first land animals were quite without predaceous enemies and were able to enjoy the benefits of sunshine by becoming diurnal and heliothermic. But increasing competition on land drove some forms into the cavern of nocturnality to escape their enemies and to be able to feed in comparative peace. These nocturnal amphibians and reptiles were the better off, the smaller their bodies and the less they were dependent upon the sun for the maintenance of rapid metabolism. The advent of small-bodied descendants of the massive stegocephalians made nocturnality desirable for the reduction of water-loss; and the small animal, being able to be more active at a given environmental temperature, suffered no disadvantage from the change in habits.

Upon the invention of 'warm-bloodedness', independence of the sun became greater. The mammals for the most part proceeded to become crepuscular and nocturnal. The defenseless plant-eaters then found greater safety in feeding, which is in them an almost continuous and decidedly noisy process which places the animal at a real auditory disadvantage. Predators were forced into nocturnality by the paucity of diurnal prey. The birds, however, were mostly prevented from abandoning diurnality by the high requirements imposed upon visual acuity by the habit of flight. The ability to fly, in itself, served as a compensatory defense against most predators, for birds are most vulnerable in the form of eggs and young, as easily captured at one time of day as another. The most conspicuously nocturnal birds, the owls, trace their ancestry from diurnal birds through the crepuscular goat-suckers and frog-mouths. They had no trouble in becoming nocturnal, for with their size and roundheadedness, there was abundance of room in their heads for eyes large enough to combine fair resolution with super-sensitivity.

Though nocturnality is something of a sanctuary from predators and carries with it a coincidental improvement of audition and olfaction

(available also, of course, to the nocturnal predator) it imposes some restrictions on diet. Tiny food objects cannot so easily be discerned, and we find nocturnal animals to be relatively gross feeders, cropping vegetation which they have located by scent, rather than pecking at seeds, and seizing large, unaware prey or motionless nestlings rather than running down minute insects. Where insects do constitute the food, they are not usually caught individually after visual location, but are 'trawled' in numbers, as by the sticky tongue of an ant-eater. Seeds are sought in numbers also—the rodents proverbially prefer their seeds in bunches, as in a head of wheat or an ear of maize.

The superior visual acuity of the diurnal vertebrate often enables him to maintain an enormous disparity between his armament and the defenses of his prey—as when a hawk seizes a garter-snake or a kingbird catches a fly. The nocturnal carnivore must have superior weapons, for he must usually fight on more nearly equal terms with relatively much larger prey. He prefers to catch nocturnal prey at a disadvantage in the daytime, and it is not surprising that carnivorous forms are as often twenty-four-hour animals as strictly nocturnal ones. The very strictest of nocturnality is seen among those preyed-upon animals which are so defenseless that they dare not come out of their hidey-holes even to bask. In this category fall most of the legions of rodents.

Lightless Habitats and their Conquest—At this point we should give a moment's attention to the fact that in addition to nocturnality 'by the clock', there are several other dim-light habits of vertebrates which might seem to call for the same ocular modifications: the fossorial habit (as exhibited by the mole, as opposed to forms like the woodchuck which live in a burrow but use it only as a home); the cave-dwelling habit (as developed by the permanent residents of caves in contrast to such animals as the bats, which use caves only temporarily; the internally-parasitic habit; the deep-sea habit; and the occupation of very muddy waters.

The habitats involved here are practically or entirely lightless, and the animals which have adopted them have, for the most part, given up any attempt to see and have allowed the eye to degenerate to a tiny, even microscopic vestige, or to vanish altogether (see also pp. 387-405, and Fig. 133). Well-developed eyes, adapted for dim-light vision, are found only in those forms which occasionally venture into one of these habitats for purposes other than mere temporary concealment; and out-

side of the vertically-wandering fishes and whales these are very few indeed. There are many other exceptions constituted by the deep-sea fishes, most of which have enormous eyes whose retention and perfection we can safely attribute to the timely invention of light-producing organs by deep-sea animals. There is some point to a retention of a sense of light and darkness by subterranean forms so that they may be aware when their burrows have been broken into by the weather or by other animals. Such animals, like the moles, marsupial moles, *Spalax,* and the fossorial reptiles always have enough of an eye to make this much 'vision' possible. But the strictly cavernicolous vertebrates, all of them fishes or salamanders, have only microscopic, completely non-functional eyes. Of the two dozen or more cave-dwelling species of fishes, only two or three ever (as individual variations) exhibit useful eyes, and in only one of these (the Mexican *Anoptichthys jordani*) do the eyes vary from zero to complete normality. The same degree of degeneracy as in cave fishes is seen in the parasitic hag-fishes, which 'burrow'—in the bodies of their prey!

As for the muddy-water problem: several kinds of gobies and at least one mammal (the fresh-water dolphin *Platanista gangetica,* swimming through the roiled waters of the great Indian rivers), have given it up as an impossible job. The eye of *Platanista* has 'gone bad' in a unique way—this is the only vertebrate with a macroscopic eye which lacks all traces of a lens. In such limicolous gobies as *Austrolethops* and *Trypauchen,* and in the sole *Typhlachirus,* the entire eye is minute or quite obsolescent. In general, the fishes of silty rivers, as in our Great Plains, have somewhat undersized eyes which are useful only close to the surface, where alone there is adequate light. The fishes of the peculiar Lake Balaton have however made a valiant effort to cling to vision despite the quasi-opacity of the water in which they swim (see p. 236).

The Eye as a Whole—It was hinted earlier (p. 172) that nocturnal animals, as well as diurnal ones, have a special need for a large eye. The need is a very direct one in the case of a diurnal eye: to enlarge the image. The reason why large eyes are desirable for a nocturnal animal is a little more complicated. It is not at all for the improvement of resolving power—a whale eye the size of a baseball has but 2% of the resolving power of the human eye, due to its tremendous retinal summation.

If we could be watching an animal in the process of evolving nocturnality, we might feel impelled to advise him to enlarge his eyes "so more light can enter them." But on second thought we should realize that this

would only tend to *dim* the image on the retina. Doubling the diameter of the eye will double the diameter of the retinal image. This will reduce the illumination per unit area of that image to one-fourth. But suppose the pupil enlarges in proportion to the whole eye. Doubling its diameter will increase, by four times, the amount of light it admits. The illumination of the retina will thus have the same strength in any and all eyes whose proportions are exactly the same, *regardless of their absolute sizes.*

An eye which is simply larger will not, then, have brighter images and greater overall sensitivity in dim light. But enlarging the pupil more yet, out of proportion to the size of the eye, will brighten the image. If the pupil is enlarged the lens must be broadened too, if spherical aberration is not to be increased. A broader iris (to make room for a larger pupil) and a broader (and proportionately thicker) lens will, in themselves, call for an increase in the absolute size of the eye if it is to remain mechanically and biologically in balance. We have arrived, by a rather devious route, at a justification for advising our nocturnally-inclined animal to enlarge his eyes—and to enlarge them in a disharmonic manner.

Enlarging the lens 'out of proportion' to the eye moves the optical center of the cornea-lens apparatus backward (Fig. 71, p. 173). When the curvature of the cornea, lens, or both is now sharpened to keep the image from receding behind the retina, we find that the anterior chamber has deepened and the image has shrunk. This shrinkage of the image is fine up to a certain point, for it accomplishes what was wished: that brightening of the image which lets the eye operate in dimmer light. The retina of such an animal being poor in cones, visual acuity is low enough in all conscience already, but it may suffer *too* much unless now the eye is enlarged harmonically still further, to spread the image without detracting from its brightness. That species is fortunate which has head-room for the development of sensitivity through eye size alone. The cat has a large eye for its size, but a proportionately small retinal image—only 38% of the diameter of that of the horse, whereas the diameter of the eyeball is 50% of that of the horse. The human ocular axis is only 1.19 times that of the cat, but man's retinal image is 1.37 times as broad as the cat's. Some small, small-eyed animals have had to do the whole job by making the lens spherical, the cornea perhaps remaining broadly curved since the lens has more to do with pulling backward, into the eye, the optical center whose distance from the retina determines the size of the image. The large-eyed carnivores such as the cats have greatly sharpened

the curvature of the cornea and thus have been able to keep the lens from becoming so large and so round as to increase spherical aberration to any disastrous extent.

The end result of the juggling of these factors is an eye which, as compared with a diurnal eye such as that of man, is:

1. Relatively large for the size of the animal, and absolutely large if there is room for it in the head—even altered in shape ('tubular' eyes—*v.i.*) if there is not space enough for an orthodox eye.

2. Provided with a relatively large anterior segment, making room for a large-opening pupil and a proportionately large lens, which is:

3. More nearly or even quite spherical and set far back from the cornea (which where convenient is less sharply curved), so that the anterior chamber is often deepened and:

4. The optical center is far back within the eye, resulting in a smaller and brighter retinal image.

'Tubular' Eyes—There are certain interesting consequences of these changes which, in themselves, add nothing to the capacity of the eye for operation in dim light. Whereas the diurnal eye tends to have a small anterior segment and a large fundus, the nocturnal eye tends to have a large anterior segment and, the image being small, would gain nothing from having a posterior segment proportioned to it as in a diurnal eye. The result is a relatively small fundus, rendering the eye somewhat tubular in some species in which the anterior segment has become enormous. This is true of the owls and their relative *Podargus,* some lemuroids, and a majority of the deep-sea fishes which have kept their eyes. These forms, so to say, have ballooned the eye to the point where there is barely room for it in the head (Fig. 84), and have continued to enlarge the anterior segment so that the effect is produced of the useless equatorial region of the globe having been cut away (Fig. 136b, p. 400). The eye of the deep-sea fish bears the same relation to a standard-shaped fish eye of the same axial length as does the part of an apple, removed by a cylindrical coring tool, to the intact apple.

The small size of the retina in tubular nocturnal eyes tends to make more narrow the angle which embraces the visual field outside of the eye. This demands considerable rotability of the eyeball in the orbit, in order that the animal shall be able to see about him through a safely wide angle. But, these tubular eyes have become so large that they are

locked in a close-fitting orbit and cannot be turned. Even though the oculomotor muscles are present in owls, the eye of an owl cannot be moved in the orbit by force. In consequence, the owls and the lowest primates *(e.g., Tarsius)* have evolved an extraordinary rotability of the head upon the axis of the body. The neck in all birds is notoriously flexible—even the strictly diurnal hawks can rotate the head about 180°; but the owls can revolve theirs through 270° or more. To explore their surroundings visually, the deep-sea fishes, lacking a neck, must turn the whole body, or bend the trunk if they are slim enough to do so.

Spherical Lenses—Where the eyes of small nocturnal animals have remained spherical and not enlarged unreasonably, the lens is always even larger in proportion than in tubular eyes. In fact, when the lens

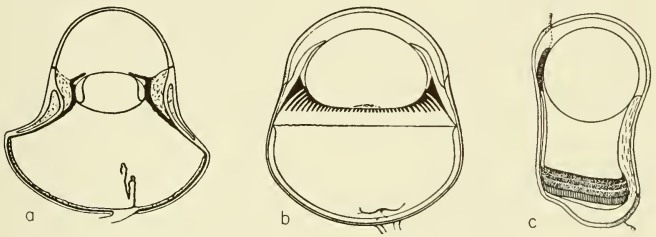

Fig. 84—Tubular (miscalled 'telescopic') eyes.

a, owl, *Bubo* sp. × 1. After Pütter. b, prosimian, *Galago crassicaudatus garnetti*. × 2.46. After Franz. c, deep-sea fish, *Argyropelecus* sp. Redrawn from Hesse.

swells (through evolution) in size it swells also in shape, so to say, and tends toward a sphere (Fig. 71, p. 173). When it has attained this shape, as in small bats, most rodents, and the rodent-like opossums, an advantage is gained in connection with the need for voluntary eye movements —the latter can be allowed to diminish or even to disappear. Part of the reason for this is the absence of an area centralis, owing either to its disappearance or to a failure to evolve one. Since there is no reason to aim any particular retinal spot at the object under scrutiny, there is no reason for aiming the eye at all. Largely, however, the diminution of eye movement is due to the periscopic action of a spherical lens when associated with a concentric or nearly concentric retina. Such a lens casts an image which is small, but is equally good from whatever direction the object

is imaged. Hence the eye with a spherical lens sees its object about as well in the periphery of the retina as in the fundus. A moving object can therefore travel farther alongside or around the head of the animal before the latter need make any movements to keep it in good view. The only extra requirement is a wide cornea, and the net result is a widened visual field.

Broad Corneæ—The effect of an extensive cornea—and some, like that of the house-mouse, cover about half the surface of the eyeball—like that of large ocular size as such, is easily misunderstood. As has been made clear, it is not true that a unit retinal area is more brightly illuminated in a large eye (*ceteris paribus*) than in a small one. This does become true only when the lens and pupil are disproportionately large. Neither does a large cornea let in more light, as is commonly supposed. It is the *pupil* which regulates the amount of light that reaches the retina. The cornea would not need to be any larger than the fully dilated pupil, if the iris were right against the cornea. To let light rays hit the front part of the retina and increase the periscopy of the eye, however, the cornea must be broader than the pupil; and the more so, the farther the iris and lens are from the cornea. Since nocturnal eyes tend to have deep anterior segments for the reasons given above, we can see that their relatively broad corneas (compare lynx and man in Fig. 71, p. 173) are a consequence of these other ocular changes, and do not in themselves promote sensitivity to light. The recession of the optical center into the eye, in strongly nocturnal forms, cannot be wholly compensated for by a broad cornea. The deeper the optical center within the eyeball, the smaller and brighter the image will be; but the farther back the center is from the pupil, the larger the pupil and the cornea must become in order to maintain a wide-angled visual field. Despite all efforts of pupil and cornea, the nocturnal eye tends dangerously toward 'tube vision'—that restriction of visual field which we experience in looking through an aperture located before the eye. The nocturnal animal, therefore, dares not rely solely upon increasing the objective intensity of the image, by manipulating its relative size through mere gross changes in ocular morphology and optics. He must keep the need for such changes minimal (since they inevitably detract from visual acuity and visual angle) by promoting the response to whatever light is available. This necessarily means increasing the sensitivity of the retina itself.

(B) The Nocturnal Retina

Rod:Cone Ratios—We expect to find rods greatly predominating in nocturnal retinæ; and we are never disappointed. However, pure-rod retinæ are not as common among strictly nocturnal animals as pure-cone retinæ are among strictly diurnal ones. Fabulous though the cat's ability may be for "seeing in the dark," she has a very respectable number of cones—about a third as many as we ourselves, who are marooned among the strongly diurnal animals when our artificial lights are taken away from us.

This persistence of cones in nocturnal retinæ calls for a little special explanation, for it has served some people as a sufficient excuse for rejecting the Duplicity Theory entirely. The first prominent opponent of the theory—Wilhelm Krause, a contemporary of its formulator, Max Schultze—saw more cones than there really were in many nocturnal forms, and drew incorrect conclusions from other animals through imperfect knowledge of their habits. Several modern investigators (particularly Mlle. Verrier) have apparently thought that if there is anything to the Duplicity Theory, then cats and owls should have no cones whatever.

This view fails to take account of the fact that whereas a diurnal lizard never gets out of bed for a midnight snack, a cat may appreciate a sun-bath at high noon. The nocturnal animal which wishes (as most do) to be able to come out sometimes in daylight, is wise to retain some cones for the improvement of form-sense, for he is otherwise at a great disadvantage if taken by surprise by a diurnal enemy.

If this interpretation seems weak, we can surrender any positive argument in favor of a nocturnal animal's keeping cones, and still believe the Duplicity Theory to be well founded. The only pure-rod retinæ are in nocturnal animals, and the proportion of cones in such animals is never very high. Where there are so few as to seem utterly useless, as in the opossum or the rat, it may be pointed out that unneeded cones are probably harder to get rid of than are unwanted rods. The vertebrate eye, like the brain, is so delicately-balanced an organ that it very rarely contains anything useless. The eye is comparable to a machinery-crammed submarine—if there is no proper niche for a thing, it is almost certain to be in the way. In a strictly diurnal eye, even a few rods can detract very immediately from resolving power, and they are completely eliminated from every good area centralis. But cones, as we have learned, keep

to themselves in the matter of their nerve-cell connections, and ten cones scattered among a thousand rods cannot cost the retina as much in sensitivity as ten rods, scattered among a thousand cones and hooked up to a single optic nerve fiber, would cost it in resolving power. There is consequently simply not the urgency for getting rid of cones in nocturnal animals, that there is for weeding out rods in diurnal forms. This is quite apart from any greater usefulness of 'even a few' cones than of 'only a few' rods. The turtles are conspicuously exceptional in having only a very few rods scattered in an almost pure-cone retina—but even these may be useful since they are more numerous in light-shunning forms such as *Chelydra,* and in the nocturnal *Pseudemys.*

Pure-Rod Animals—A pure-rod retina is automatically obtained where, as in some lizards (geckoes, etc.) and snakes (*Hypsiglena, Phyllorhynchus*) it has been manufactured by transmuting all of the single and double cones of an ancestral pure-cone retina into single and double rods. Transmutation has left so very few unchanged cones in *Sphenodon* that in an entire section of its very large eye, never more than twenty can be found. Aside from these forms, absolutely cone-free retinæ which once were duplex, and have lost their cones, are known for a certainty to occur only in deep-sea fishes, the bats, and the armadillo. Some others probably have only rods—all but one or two elasmobranchs, *Lepidosiren* among the lungfishes, cæcilians, the hedge-hog, the guinea-pig, the whales and seals, most lemuroids and *Aotus*—but all of these need additional histological study (since most of these were last studied, microtechnical methods have improved enormously). Still others, like the rat and other nocturnal rodents, are widely believed to have no cones but do indeed have a few. One ridiculous statement often seen is that rats and owls "have a few rudimentary cones." In a duplex retina, no visual cell is ever rudimentary, though one *population* of visual cells may be so scant as to deserve the term, like the cones of *Sphenodon* or the rods of turtles. As a matter of fact, owls have enough cones so that they are able to see more acutely by day than by night. Rochon-Duvigneaud once picketed a *Bubo bubo* in an open field, and found that it could detect an approaching hawk which was flying so high as to be invisible, at that moment, to humans.

Summation—In nocturnal animals the rods tend to be very slender as well as very numerous, causing the outer nuclear layer to thicken greatly (Fig. 72, p. 177). In lungfishes and amphibians, however, the rods are

bulky and exceed the cones in total volume as well as in actual numbers (Fig. 64, p. 148)—just as in most teleosts the huge cones outweigh the more numerous, tiny rods (Fig. 94, p. 237). The difference in acuity-performance of bulky cones versus slender ones is obviously very great, for the retinal limit of resolving power is set by the distance on centers between the cones. It is not so easily apparent why nocturnal animals should have slender rods and other animals not only fewer but plumper ones. The slenderness of a rat's rods has not been produced for its own sake. The distance between centers of adjacent rods has nothing to do with the overall sensitivity of the rod population—but the number of rods which can conveniently be hooked to a bipolar cell (this being promoted by slenderness and close aggregation) has everything to do with it. In amphibians and lungfishes not only the visual cells but most somatic cell-types are notoriously huge. It makes an interesting speculation: did the unknown factor which made their cells so large doom the amphibians forever to low visual acuity because their cones are usually bulky, and to a not particularly high sensitivity also, because their rods are so big?

The thick outer nuclear layer resulting from the slenderness of nocturnal rods (the tiger holds the record here!) is pretty well counterbalanced by the thinning of all other retinal layers due to the great extent of summation of visual cells in bipolars, and of these in ganglion cells, for the sake of sensitivity and at a tremendous sacrifice in resolving ability. Nocturnal animals, on the whole, have thinner retinæ than diurnal groups, and have much more slender optic nerves. It is not at all unusual for several thousand rods to be summated in one optic nerve fiber. The retinal adaptations for sensitivity, both within the visual cells themselves and in their relationship to optic nerve fibers, render the receptive tissue of a nocturnal animal so extraordinarily sensitive to light that it cries out for protection from any light stronger than that of the moon. We go on now to consider how this protection has been obtained.

(C) The Slit Pupil

The elementary discussion of pupil mobility in section C of Chapter 7 was based upon the commonest form of the aperture—the circle. There are a number of departures from this primitive shape, the most widespread one being the slit, which in land animals, at least, is most commonly vertically oriented, for which a reason is given later (see p. 428).

Value of the Slit Form—The slit pupil, like nearly all pupils, dilates in dim light to a perfect or almost perfect circle. Very many years ago, a generalization had already been found possible, to the effect that the slit pupil is associated with nocturnal habits. Yet under nocturnal conditions the slit pupil becomes as round as any. Obviously it has nothing to do with vision in dim light; what then does it accomplish?

The broadly oval pupil of a frog can contract to a diameter which is one-third of its fully dilated size; but to bring about this degree of contraction, the intensity of light must be increased 200 times. We have

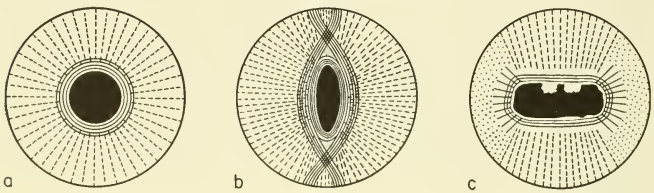

Fig. 85—Diagrams of mammalian iris musculatures.

a, round pupil of diurnal and strictly nocturnal forms, showing simple sphincter (solid lines) and symmetrical dilatator (broken lines).

b, vertical slit (of cat), characteristic of nocturnal forms which bask. Part of the sphincter surrounds the pupil, but two bundles which cross above and below and continue to the periphery have a scissor-action upon the pupil, compressing it laterally. The dilatator (broken lines) is quite symmetrical—contrast Figure 88, page 223. Redrawn from Raselli.

c, horizontal pupil (of horse), characteristic of ungulates, some whales, and other species. Some sphincter fibers are oriented radially and are anchored in connective-tissue sectors (stippled) which are devoid of dilatator fibers (broken lines). The pupil can expand to a circle; but when the sphincter fibers contract, the terminal ones force the pupil to become a horizontal rectangle, indented by the corpora nigra (white). Based upon drawings and descriptions of Eversbusch.

already noted that the frog is more dependent upon the photomechanical changes of its retina for avoiding dazzlement in bright light. His pupil cannot cope with the situation; but for that matter, neither can any pupil *whose closure depends upon a ring-shaped, sphincter muscle.* We ourselves can easily be dazzled even when our pupils are closed as far as they will go. True, a lizard or a garter-snake is comfortable in even brighter light despite the practical immobility of the pupil—but these forms have only the relatively insensitive cones in their retinæ.

Where the rods are very much in the ascendant, the circular pupil ceases to be adequately protective. The sphincter may contract fully, but

even then it has considerable length, for it cannot eliminate itself entirely. The arrangement of the iris muscles around a slit pupil, however, is such as to make it easy for the slit to be closed without any impossible degrees of muscle contraction—closed entirely in some instances, or in any case to so small an area that the pupil is far better able to keep pace with intensity-changes than it is in the frog or even in ourselves. (Fig. 85a, b).

The slit pupil is hence in a sense paradoxical, for though it is an adaptation to nocturnality it has nothing whatever to do with seeing in dim light. Hosts of nocturnal species do not have such a pupil, and are well able to see under scotopic conditions. They get along with a circular pupil because they are content to stay out of bright light. Any strongly nocturnal, rod-rich animal which cares or dares to venture out in the sun, —whether a cat stalking the barnyard sparrow, a gecko seeking flies, a

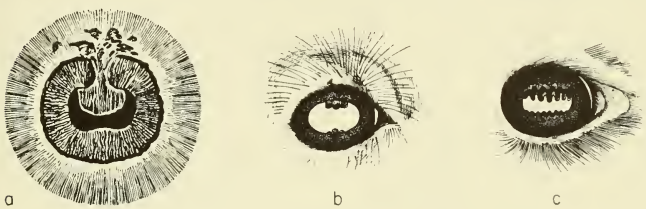

Fig. 86—Pupil shades in mammals. After Lindsay Johnson.

a, 'umbraculum' (operculum) of hyrax, *Procavia* (an analogous structure occurs in many whales). b, corpora nigra of *Gazella dorcas*. c, corpora nigra of camel.

snake seeking warmth, or a shark basking at the surface—needs a slit pupil and will be found to have one.

Even some diurnal and arhythmic animals have devices for shielding the pupil from intense glare coming directly downward or reflected upward from the ground. Among such devices are the pigmentation of the upper cornea in surface-loving needle-fishes and in *Torpedo,* the expansible pupillary opercula of some fishes and whales (Fig. 65, p. 158), the (voluntarily?) expansible 'umbraculum' above the pupil of the hyrax, and 'corpora nigra' along the pupil margins of ungulates (Figs. 85c, 86).

Distribution and Meanings of Pupil Shapes—Phylogenetically, the slit pupil is first met with in the elasmobranchs (Table VI, next page), the only group of fishes whose pupils have much contractile excursion. Most sharks have practically circular pupils, and a slit is characteristic

TABLE VI—CONTRACTED PUPIL SHAPES

			ROUND*	VERTICAL	HORIZONTAL	OTHER
FISHES	Cyclostomes (Lampreys)		+			
	Elasmobranchs	Chimæras and Sharks	+ in most	Slit (*Prionace glauca*)	Slit (*Selache maxima*)	Diag. slit, some sharks
		Skates and Rays	+ with operculum (except in mantas)	Slit (*Dæmomanta alfredi*, *Cephaloptera giorna*)	*Torpedo* has slender oblong, divisible by operc.	
	Chondrosteans and Holosteans		+	Ellipse (Sturgeons only)		
	Dipnoans and Cladistians		+		Slit; **Protopterus annectens* (no iris muscles!)	
	Teleosts	Most	+, contractile in but few (e.g. eels, *Enchelophis*)	Ellipse, *Piabuca* (only?)	Often pyriform, with anterior aphakic space	
		Flatfishes and other upward-lookers	+, often with operculum			
AMPHIBIANS		Anurans	+ in strictly aquatic spp.	Slit in a few	Broadly oval in most	Various (see figure)
		Urodeles and Cœcilians	+			
REPTILES		*Sphenodon*		Slit		
		Crocodilians		Slit		
		Turtles	+ (not contractile)			
	Lizards	Geckoes, including eublepharids and *Uroplatus*	+ (*Phelsuma*, *Lygodactylus*, some *Gonatodes* and *Sphaerodactylus spp.* only)	Slit, usually with notched margins: ‡		
		Xantusiidae, Pygopodidae		Slit		
		All others (diurnals)	+			
	Snakes	Boidae, Illyssiidae, Uropeltidae		Slit		
		Xenopeltis	+			

REPTILES	Snake	Colubridae	Nocturnals		Slit; in *Arizona*: ○		
			Dryophis & *Thelotornis*			Keyhole (⊂) with anterior aphakic space	
			All other diurnals	+	Slightly oval (*Farancia*)	Oval (*Ahætulla*, *Masticophis*, et al)	
		Elapidae		+ (very small in sea-snakes out of water)	Slit (*Acanthophis*, some *Bungarus spp*, only)		
		Amblycephalidae			Slit		
		Viperidae, Crotalidae			Slit	Broadly oval (*Causus*, *Atractaspis*, only)	
BIRDS				+ in nearly all	Slit (*Rhynchops niger*, only)	Slightly oval in a few	□ (*Aptenodytes patagonica*, only)
MAMMALS	Placentals	Monotremes		+			
		Marsupials		+ in many or most	Slit (*Trichosurus*, *Dasyurus*, et al)	Broadly oval in some macropodids	
		Insectivores etc., Bats, Edentates		+ (pinhole in *Cholœpus didactylus*)			
		Rodents and Lagomorphs		+ in nearly all (pinhole in *Pedetes*)	Ellipse (*Myopotamus*, *Cuniculus paca*, *Hydrochœrus*)	Slit (*Glis* only) Broadly oval (Marmots, *Zenkerella*)	
		Carnivores	Large	+			
			Small	+ in some	Slit or ellipse in many	—○— (*Paradoxurus*) Oval (*Cynictis*, *Suricata*, *Herpestes*)	
		Seals			Slit		Diag. slit, *Phoca barbata*
		Ungulates, etc.				⊂⊃ (corpora nigra) Slit (*Hippopotamus* only)	Umbraculum (Hyrax)
		Whales				Oval, with operculum (espec. odontocetes)	
		Primates	Lower	+(*Indris*, *Lemur*, et al)	Slit in most	Broadly oval in *Tarsius*	
			Higher	+			

* or practically round
** when freshly liberated from cocoon; otherwise, round

only of those forms which come frequently to the surface or into shallow water—*Scylliorhinus, Lamna, Selache,* etc. Most of the elasmobranchs whose eyes aim strongly upward are among the Batoidei—the skate-ray-torpedo group. With the exception of the mantas, the batoids have opercula (Fig. 65a, b; p. 158), which slope downward and slightly outward over the pupil, and expand in bright light to block the aperture. The opercular margin may be serrated, as in *Raja,* or smooth as in *Dasyatis.* It is not unusual for rays to bask at the surface in summer, and they are then exposed to especially strong light, considering the fact that their retinæ are pure-rod. The monk-fish (*Squatina,* a sort of imitation ray which is really a shark) and the electric ray *Torpedo* have slits—horizontal in the latter as in *Selache* and *Sphyrna,* diagonal in *Squatina* as in *Scylliorhinus, Lamna, Orectolobus, Gingylostoma,* etc. At least one shark (*Prionace glauca*) and some rays (*e. g., Dæmomanta alfredi, Cephaloptera giorna*) have pupils which close to vertical slits. Deep-sea forms, like the less nocturnal of the littoral and pelagic species, naturally have roundish pupils, which in *Etmopterus* and the chimæras are extremely large and are practically immobile. The slit form of pupil is well established in the elasmobranchs, but in this group its orientation has never settled down to the vertical position which is almost universal in land animals for a reason which will appear later.

No chondrostean, holostean, or teleostean fishes have slit pupils, though those of *Acipenser* and *Piabuca* are broad ellipses, with the long axis vertical and with more or less of a point at each end. In the American shovel-nosed sturgeon (*Scaphirhynchus platorynchus*) the pupil is a canted square with rounded corners. Only a very few teleosts (*e. g., Anguilla, Encheliophis*) have contractile pupils. The retinæ of teleosts, except in deep-sea species of course, are never pure-rod as are those of practically all elasmobranchs; and moreover they have the photomechanical changes to rely on. The pupillary opercula present in many flatfishes, and ir others (*e. g., Plecostomus*) which live on the bottom in shallow water, are in the same category as the umbraculum of the hyrax—these devices are parasols for diurnal eyes which are exposed directly to high intensities. Their mechanism of expansion has yet to be elucidated. In one of the batfishes, *Halieutichthyes aculeatus,* fixed superior and inferior opercula overlap as the pupil closes (taking three seconds or so to do so), and the end result is about as in *Scylliorhinus* (Fig. 91, p. 225).

One lungfish, *Protopterus,* has a most peculiar pupil: the iris is quite devoid of muscle elements, and yet the pupil can become a narrow hori-

zontal slit. It has this form for a few hours, at least, after the animal is released from its mud-ball or æstivational cocoon. Eventually, however, it rounds up and thereafter remains circular in all illuminations. Another lungfish, *Lepidosiren*, has a small circular pupil which never changes; but this fish has been claimed to have photomechanical changes in the retina.

Among the amphibians, the salamanders and cæcilians all have round pupils suited to their secretive and fossorial habits. Most anurans have

Fig. 87—Shape of the contracted pupil in different amphibians.

(All are circular when dilated. From various sources; right eyes; not to same scale).

a, urodeles and aquatic anurans (Pipidæ *et al*). b, most anurans. c, *Hyperlius horstockii*. d, *Polypedates reinwardtii*. e, *Corythomantis greeningi, Aparasphenodon brunoi,* and *Trachycephalus nigromaculatus*. f, several anurans (see text). g, *Scaphiopus* and *Phrynomerus*. h, *Hyla vasta*. i, *Bombina*. j, *Pelobates fuscus*. k, *Calyptocephalus quoyi*.

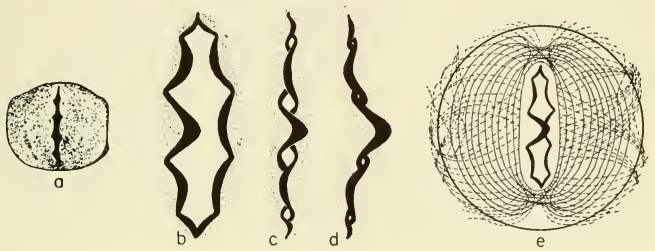

Fig. 88—The gecko pupil.

a, eye of a gecko in diffuse daylight. × 5. After Beer. b, c, d, stages in the contraction of the pupil of the right eye of *Tarentola mauretanica*. After Läsker. e, iris musculature of *T. mauretanica* (combined from two figures of Läsker). Sphincter fibers suggested by solid lines, dilatator fibers by broken lines. Note that some sphincter tracts surround the pupil concentrically and others eccentrically, while still others have a closed circuit in either the nasal or the temporal half of the iris.

horizontal, broadly oval pupils. The rigidly nocturnal spade-foot toads (*Scaphiopus*), and the brevicipitid genus *Phrynomerus* also, have an approach to the vertical slit in their beautiful lozenge-shaped pupils. The vertical slit occurs in quite a number of nocturnal anurans—in *Alytes obstetricans*, several criine toads, *Lymnomedusa, Phyllomedusa* and several other hylines, some polypedatids, and *Hypopachus*. The Javanese flying-frog, *Polypedates reinwardti,* has a slender horizontal slit, while

others in its family have vertical slits or broad, horizontal ovals. The pupil is heart-shaped in *Bombina,* rhomboidal in some hylids, and may take on still other peculiar forms (Fig. 87).

The crocodiles, all notorious baskers, have the vertical slit. So does *Sphenodon,* in which it is tilted a bit out of plumb. The turtles are a diurnal group with insensitive retinæ and immobile, circular pupils. Most lizards are diurnal and have round pupils; but several families of lizards are night-prowlers and have vertical slit pupils—among them perhaps the most remarkable of all pupils, that of the majority of the geckoes. This pupil customarily has several tiny notches paired off along its opposite margins. When brightly lit, the pupil closes completely, leaving a series

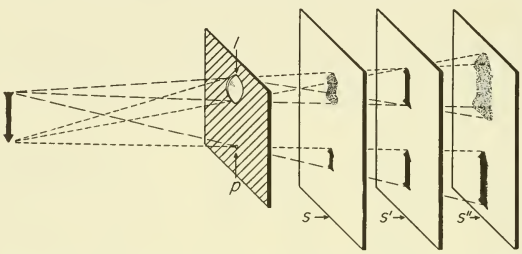

Fig. 89—Pinhole compared with a lens, as a means of forming an image.

Note that the resolution of the pinhole image depends less upon a critical location of the screen; but the lens image is much brighter since the lens admits more light.

l- lens; *p*- pinhole; *s, s', s''*- position of screen.

of pinholes formed by the apposed notches (Fig. 88). Each of these pinholes is so small that it serves as a stenopaic aperture, forming a sharp image all by itself just as though the lens and cornea were not there, and moreover making accommodation quite unnecessary since it forms fairly sharp images, simultaneously, of objects at various distances (see p. 256 and Fig. 89). Insufficient light gets through any one of the pinholes to stimulate the retina adequately. Since however the images formed by all of them are superimposed on the retina, their total illumination is sufficient. At the same time, the image is sharper than it would be if formed by a single aperture, equal in area to the sum of the pinholes; and no sacrifice of the width of the visual field is entailed (see Fig. 90, especially c). Something of the same effect is obtained by *Scylliorhinus* (Fig. 91) and

Raja (Fig. 65a, b; p. 158), and by a number of other animals (*v. i.*).

Among the snakes, the vertical pupil is seen in all nocturnal forms excepting very secretive burrowers (*e. g.*, coral snakes) and the cobras, whose nocturnality is far from perfect. All boas and pythons, all pit-vipers, and all vipers except such primitive and crepuscular forms as *Causus* and *Atractaspis,* have the slit. So also with a few elapids (*e. g.*,

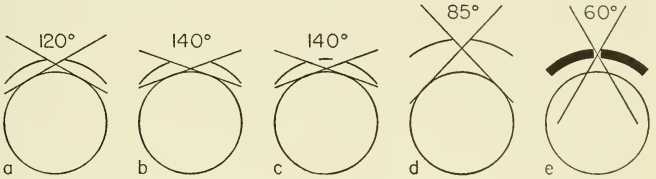

Fig. 90—Effect of variations in the pupil. Modified after Franz.

a, standard of comparison. b, the pupil has been doubled in width, hence quadrupled in area; but the visual field is thereby only slightly enlarged. c, the multiple pupil, whose effect is to reduce the brightness of the image and improve its resolution, without sacrifice of field width. d, narrowing of field owing to separation of pupil and lens. e, narrowing of field owing to thickening of pupil margin.

Acanthophis, Bungarus) and a considerable number of colubrids, particularly back-fanged species. In short, all strongly nocturnal snakes which ever voluntarily hunt or bask in bright light have vertical slit pupils. In some secretive and crepuscular forms, shapes intermediate between the round and the slit forms occur. Thus in the rainbow snakes

Fig. 91—Eye of a shark, *Scylliorhinus canicula;* external view, and stages in the contraction of its pupil. Redrawn from Franz. *n*- nasal side; *t*- temporal side.

the fully contracted pupil is a broad vertical ellipse, and in *Arizona* it contracts to the shape of an egg with the narrow end pointing downward. Diurnal snakes nearly all have round pupils, though three or four tree-snakes (*e. g.*, *Ahætulla picta*) have horizontally oval ones; and in three colubrid genera there is a horizontal keyhole of special significance which may divide into two ovals when it closes (see pp. 185-6 and Fig. 79).

Only one bird, the black skimmer (*Rynchops nigra*) is known to have slit pupils, despite vague mentions, in popular and even highly technical literature, of such pupils in owls. The pupil is most peculiar in *Rynchops,* in that the two halves of the iris seem to swing inward independently, like a pair of gates, to form the slit. One can understand the presence of a slit pupil in a sea-bird—the surprising thing is that there are not more such cases. Water of any depth is a dim-light environment, calling for extra retinal sensitivity; and it is observed that the pupils of diving birds are more responsive to light than those of others. The penguins have a great range of pupil size. Contracted penguin pupils are never quite round, and they can all become very small. That of the king penguin, *Aptenodytes patagonica,* contracts to a perfect square, dilating through a succession of polygonal shapes, like an iris diaphragm, to a huge circle. It opens widely at night or when the eye is shadowed in daytime (though the pupil of the other eye may then be a mere speck), and it presumably dilates widely under water. Penguins dive deeply out of sight; and Brandt's cormorant has been trapped at forty meters, where the light is much reduced, and is believed to go even deeper.

The skimmer does not have its sensitive eye and slit pupil for underwater vision, however. Simple nocturnality seems to be the whole explanation—the bird rests in coves by day and goes to sea in the evening to feed all night. If this one nocturnal bird species can have a slit pupil, it is perhaps strange that the owls, oil-birds, snipes and so on have failed to produce one. The skimmer is scarcely the 'logical' species to be an exception in this regard, whether it be compared with nocturnal land birds or with other oceanic birds. One would rather expect the genus of the boobies, *Sula,* to have taken the lead here:

The red-footed booby, *S. sula,* is called by Robert C. Murphy the most nocturnal of all sea birds. It has a notably larger eye than any other bird in its family, but it does not have a slit pupil. A close relative, *Morus* (=*Sula,* in part) *bassana,* the northern gannet, has been netted in twenty-seven meters of water. One peculiarity of booby pupils mentioned by one or two authors is the apparent sexual difference in size, the female seeming to have a much larger pupil than the male. If true, this would suggest a sexual difference in retinal sensitivity or eye-size; but Dr. Murphy explains it as an illusion caused by a ring of black blotches at the pupil margin of the otherwise yellow iris of the female. The male iris being entirely yellow, the pupil seems smaller and more regular. *Sula nebouxii* shows the feature strikingly; probably other boobies have it.

The monotreme mammals are secretive and nocturnal, and have round pupils. Among the marsupials, the kangaroos and wallabies are practically arhythmic, and many have oval (horizontal) pupils. New-world marsupials, and many Australian ones, have round pupils. Other Australian species have the vertical slit. O'Day finds that some marsupial pupils, usually described as round, do finally take on the slit form as the light becomes sufficiently intense. *Dasyurus viverrinus* shows this well; but the pupil of the more strongly nocturnal *Trichosurus vulpecula* becomes a small vertical slit even in diffuse daylight of ten to twenty foot-candles, at which intensity the *Dasyurus* pupil is still circular.

The placental mammals as a whole are crepuscular and nocturnal, and shun bright light. The hoofed animals and the great cats are arhythmic, while many primates, most squirrels, and a small handful of other scattered genera (*Ochotona, Zenkerella, Suricata,* etc.) are diurnal. Though the squirrels include strongly nocturnal forms (the flying squirrels) as well as sun-worshippers, they all have round or slightly oval (horizontal) pupils. In some of the ungulates—the camel family especially—the corpora nigra of the upper and lower pupil margins (Fig. 86) can meet or interdigitate in very bright light, perhaps forming useful stenopaic apertures. In others the pupil never approaches a slit form, but can best be described as horizontally rectangular; and it may have only slight mobility, as in the horse. The pupil of a young horse is round, but at five or six years of age it becomes elliptical and the corpora nigra become pronounced, three or four of them on the superior border and five or six smaller ones on the inferior border of the pupil. The sheep, with as many as twenty corpora nigra, has the maximum number of these bodies.

Large carnivores have round pupils. The foxes, all Viverridæ except *Cynictis* and *Suricata,* and one or two rodents have vertical ellipses. Outside of the prosimians, a fully closable slit is seen in mammals only in the smaller cats, the strongly nocturnal and arboreal toddy cat or palm civet (*Paradoxurus*), and the dormice (*Glis* spp.). *Paradoxurus* is exceptional in having a horizontal slit, which has a single pair of central notches on its margins which form a single stenopaic aperture when the remainder of the pupil closes entirely. Two other viverrids, *Cynictis* and *Suricata,* have horizontally oval pupils on the order of those of ungulates. *Suricata,* peculiarly vegetarian for a carnivore and rather marmot-like in its behavior, is said to be diurnal.

In the cats and dormice the vertical pupil can also close entirely, leaving, in the domestic cat at least, a pair of terminal pinholes reminiscent

of those in *Scylliorhinus*. Seals have vertical slit pupils, excepting in one species (*Phoca barbata*) whose slit is diagonal—indeed, almost horizontal as is the slit in *Paradoxurus* and in the hippopotamus. But the seal's pupil, as will be made clear later, needs its slit form for a reason quite different from the one which accounts for probably every other slit pupil in the vertebrates.

The history of the primate group has been one of increasing diurnality from strictly nocturnal beginnings, with 'successfulness' increasing along with the tendency toward diurnality. The range in size from the timid, nocturnal, three-inch mouse galago to the monstrous, diurnal gorilla is most striking. All but one of the lowest prosimians (the bush-babies, lorises, etc.) have vertical slit pupils. The true lemurs (genus *Lemur*) have vertical pupils which are not at all slit-like, but only slightly oval. They and their closest relatives (*e.g., Indris*) do all of their sleeping at night. All of the simians (monkeys, apes and man) except *Aotus* are diurnal, with the great apes most strongly so. The eyes of some prosimians are so sensitive that, despite the protection afforded by the slit pupil, they are prone to undergo retinal degeneration and to become blind when, in zoos, they are kept in too strong light. Similar changes are said to occur, by the way, in nocturnal birds, fruit-bats, and some bears.

Tarsius is the one primitive lemuroid which does not have the slit; but the pupil in this genus has an enormous excursion from a large circle to a broadly horizontal oval only half-a-millimeter in diameter. In its range of sphincter-length, the tarsier's iris has a very few close rivals: those of the two-toed sloth, the African jumping hare (*Pedetes*), the sea-snakes, and the pearl-fish (*Encheliophis*). One suspects that in such animals the sphincter must have some special organization; but the details are as yet unknown. They have somehow found the secret of obtaining an extremely small pupil-area without resorting to the slit form, or to the even more elaborate device of an expansible operculum.

(D) The Tapetum Lucidum

The standard condition of the chorioid coat is one of heavy pigmentation. The pigment epithelium may or may not contain much pigment also, depending chiefly upon whether this pigment is migratory or not. It is the pigment of the chorioid, alone, which has the real responsibility of preventing reflections within the eyeball which might blur or even multiply the image.

The light rays which are focused by the dioptric apparatus and pass through the retina are never completely absorbed by the chorioidal pigment. If they were, the ophthalmoscope would never have been possible. With this instrument the observer looks along a beam of light which is directed through the pupil of the eye of the subject. Enough of the light is reflected from the subject's eyeground, directly back into the eye of the observer, to enable the latter to see something of the retina and the inner surface of the chorioid of the subject, magnified by the subject's own cornea and lens.

So bright a light as that of the ophthalmoscope does not often enter the eye directly, and the fraction of more ordinary illumination which reflects from the chorioid is too weak to blur the principal image and detract from visual acuity. The photographer has to rely on essentially the same phenomenon. He has a right to expect that the dead-black lining of his camera will reflect practically no light through or upon the film. When such reflection does affect the film due to some defect in the camera, the picture is blurry with the unwanted light and the photographer calls the result 'halation'.

Value and Basis of Eyeshine—There is one circumstance in which one might conceivably strive to produce a very maximum of halation: when the light-intensity is extremely low and a correspondingly lengthened exposure is for some reason impossible. Cameras have occasionally been built, in which the emulsion of the plate is on the back surface and is in contact with a layer of bright mercury. This layer forms a mirror, reflecting the light back through the emulsion and thus increasing its effectiveness.

When a biologist is asked to account for the phenomenon of 'eyeshine' in animals he may give the flip explanation: "they do it with mirrors"—and have every assurance that he is actually being perfectly matter-of-fact and scientifically accurate. When we consider how brightly the eyes of many animals reflect the light of our headlights as we drive past them at night, it is apparent that these species must be reflecting light back through their retinæ instead of absorbing it in a typically pigmented chorioid. Ophthalmoscopic and histological investigation bears out this suspicion, and usually discloses a special mirroring device located somewhere behind the rod-and-cone layer. Though it is very differently constituted in different cases, this mirror is generically called the *tapetum lucidum*. This apt term means, literally, 'bright carpet'. The tapetum is

required by some vertebrates because of an important difference between a camera and an eye: for the eye, exposure-time cannot take the place of intensity—the eye can only take 'snapshots'.

Under nocturnal conditions, a visual object may be brighter than its surroundings, or it may form a shadowy silhouette against a background brighter than itself. There is a perennial argument as to whether a tapetum enhances visibility by sometimes promoting the perception of the object, or by sometimes increasing the apparent brightness of the background. The argument is quite pointless; for, no matter which has the greater brightness—object, or ground—the reflections from the tapetum will increase the absolute and relative differential between the two, and thus increase their discriminability.

Not all animals which have eyeshine possess any definite tapetum, as an examination of the pertinent Table VII (pp. 240-1) will show. In the ostrich, at least, the light reflex has been attributed to the lamina vitrea between pigment epithelium and chorioid, as the lamina is extraordinarily thick in this bird. A number of other birds, both nocturnal and diurnal, also show eyeshine, but with no known structural basis for it. There are also many fishes, anurans, and snakes (but not lizards) in which there is eyeshine and in which the reflecting material has not been identified, though it is certainly nothing especially differentiated for the purpose.

An anomalous eyeshine even occurs in a few humans. It is normally lacking in all diurnal monkeys and apes, and Ernest Walker found only a "faint suggestion of a shine" in the diurnal *Lemur catta.* Among the other mammals, the rodents and lagomorphs are conspicuous for having a dull eyeshine (whose basis is yet to be found) in nearly all species, including even the strongly diurnal squirrels. Only one rodent, *Cuniculus paca,* is known to have a tapetum; and even here the reflex is said to be of only moderate brilliance. The Hystricidæ may prove to have a tapetum of some sort, for in these exotic porcupines the silvery eyeshine is described as being particularly brilliant, and visible through a wide angle.

In snakes, the eyeshine varies from faint to brilliant in both diurnal and nocturnal groups. Klauber states that it can be seen through only a narrow angle, which suggests that it may come wholly from the myelinated optic-nerve head and means nothing to the scotopic vision of the animal.

Wherever special tapeta have been constructed for reflecting light back through the visual cells, they are most often located in the chorioid coat just behind the retina; but they may be retinal, placed in the pigment epithelium of the retina itself.

The light reflected from a chorioidal tapetum, of either the 'fibrosum' or 'cellulosum' type (*v. i.*), is ordinarily seen only if the observer is stationed beyond the animal's near point. With large animals which have little or no accommodation, this means not closer than from eight to twenty feet. The light is always colored though unsaturated, sometimes so greatly as to appear almost white; and the hue may be situated practically anywhere in the spectrum except in the violet. The color may vary within a species or even, from moment to moment or from day to day, in the same individual. Such variations are unquestionably due to fluctuations in the amount of blood in the choriocapillaris, in the amount of rhodopsin present, etc., through which the light reflected by the tapetum must pass to escape again from the eye. The fundamental color thrown back from a chorioidal tapetum owes its hue to the interference of light, for it is a surface color like that of a beetle's wing-cover, a parrot's feather, or a film of oil floating on water. The hue depends upon the microscopic dimensions of the reflective elements and has no biological significance as far as one can tell.

Retinal tapeta usually appear pure white ophthalmoscopically, though the eyeshine of crocodilians is said to be pinkish-orange (and extremely brilliant in *Caiman sclerops*). *Didelphis virginiana* is also described as having a tinted (orange) reflex. With retinal tapeta, the glow can still be seen when one is very close to the animal—less than a foot, in crocodilians, if one cares to go that close. The whiteness of retinal tapeta makes it possible to see, ophthalmoscopically, the red shimmer of rhodopsin against the background of the tapetum in a dark-adapted specimen. Rhodopsin was first seen in this way, in the living eye, in crocodiles and in a freshwater fish, the European bream (*Abramis brama*).

The Tapetum Fibrosum—The simplest kind of tapetum lucidum is the *fibrosum* type. Nearly all hoofed animals have this kind, most tapeta fibrosa are in such animals, and none of them has any other kind. A portion of the thickness of the chorioid, just outside of the choriocapillaris layer, has simply been converted from an areolar type of connective tissue to a tendinous sort, and glistens just as does a piece of fresh tendon. The tapetum fibrosum is composed of dense, regular,

fibrous tissue, with the pigment cells and large blood vessels proper to the chorioid cut down locally to a minimum or eliminated. Of necessity, chorioidal tapeta are perforated at intervals by capillaries running vertically through their thickness to supply the choriocapillaris (Fig. 92b, *c*). The arborizations of these into the choriocapillaris are visible with the ophthalmoscope as stellate black dots on the bright background of the tapetum—the so-called stellulæ Winslowi.

The tapetalized area of the chorioid, in most ungulates and carnivores (which together include a great majority of all tapetum-bearing animals) is roughly a triangle with its base horizontal, and either including or avoiding the disc. The rounded apex, in the superior part of the fundus

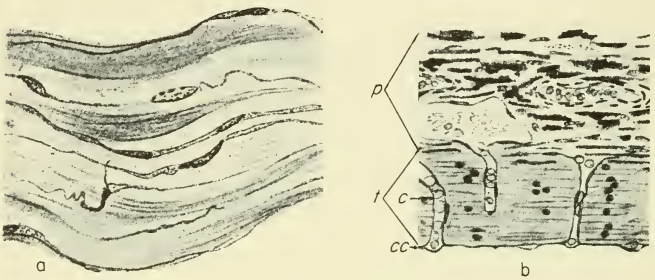

Fig. 92—Mammalian tapeta lucida, histological. From Franz, after Murr (MS).

a, bundle of fibers from tapetum fibrosum of the ox, *Bos taurus*. b, chorioid of *Vulpes vulpes*, showing modification of inner layers to form a tapetum cellulosum.

p- pigmented portion of chorioid; *t*- tapetum cellulosum; *c*- capillary supplying choriocapillaris; *cc*- choriocapillaris.

of the retina, makes about a right angle and the other two corners are not much less broad—being a spherical triangle, the tapetum can of course have angles totalling much more than 180°. The fibers of the tapetum are arranged in close-set concentric rings so that the entire tapetum is a single many-layered whorl of spindle-shaped fibers. Over the region occupied by the tapetum, the retinal pigment epithelial cells are devoid of pigment granules, thus interfering minimally with the passage of light back and forth through them.

A tapetum assignable to the fibrosum category, though of course independently evolved, is known in a few fishes and will no doubt eventually be found in many others. Our American fishes are most im-

perfectly known, ophthalmologically speaking. Such forms as the moon-eye (*Hiodon*) probably have tapeta of some sort, possibly tapeta fibrosa; but they have not yet been studied.

At least two or three of the marsupials have produced tapeta fibrosa. Those of the elephants and whales, however, may be genetically related to the tapetum of the ungulates, of which both groups are sometimes considered to be remote kin. In the broadest sense of the term, the elephants *are* ungulates. The whale tapetum differs from that of a hoofed creature only in being thicker and more extensive in area, though it is usually restricted to the superior half of the retina.

The excellent tapetum fibrosum of *Aotus* (= *Nyctipithecus*), whose

Fig. 93—Tapeta lucida in surface view.

a, fundus of carnivore (dog; right eye), showing characteristic shape of tapetum cellulosum (hatched) and usual location of disc (stippled); the tapetum fibrosum in ungulates has about the same extent, but is more rounded dorsally and tends toward a semicircle in shape. Redrawn from Preusse. b, single cell from tapetum cellulosum of domestic cat, showing rodlets of reflective material. Redrawn from Murr. c, shape and extent of tapetum of the common opossum; the drawing could serve fairly well to represent the whales and the one tapetalized rodent, *Cuniculus paca;* but the tapeta of seals are even more extensive.

eyeshine is reported to be more brilliant than that of the cat, represents another independent concoction of the fibrosum type. These douroucoulis or night-monkeys are the only nocturnal Simiæ—thus, the only nocturnal New World primates—and the tapeta of the Prosimiæ belong to quite another category:

The Tapetum Cellulosum—Besides the tapetum fibrosum, another equally widespread chorioidal type is the tapetum *cellulosum.* The nocturnal prosimians (whose eyeshine is especially vivid), all but two species of the great order Carnivora, and all of their close relatives the seals, have been found to possess this more complex type. The glorious eye-

shine of the domestic cat has been known literally for millennia: it was the basis of the reverence shown the cat by the ancient Egyptians, who believed that the cat's eyes magically reflected the sun even at night when it was hidden from mere man. Although the typical carnivore tapetum is the same large triangle as the tapetum fibrosum of an ungulate (Fig. 93a), and resembles it ophthalmoscopically even to the presence of the 'little stars of Winslow', it is very different histologically and in evolutionary origin:

Endothelial cells, such as lurk in the meshes of any chorioid, have proliferated just outside of the choriocapillaris to form several layers of thin, broad, tile-like cells (Fig. 92b). Unlike the arrangement of cells in a true stratified epithelium, there is a tendency in the tapetum cellulosum for the boundaries of each cell to coincide with those of cells in the layers immediately above and below—in other words the courses of brickwork are not staggered. The connecting capillaries, running to the choriocapillaris from vessels in the outlying, normally vascular, pigmented layers of the chorioid, can consequently take quite straight paths and thus interfere but little with the action of the tapetum.

The number of layers of cells may be only four or five, as in the wolverine, or as many as 15 as in the cat (the dog has 10, the lion 8 to 10). The numbers are higher in the seals, however, ranging from 16-18 to 30-35 (in *Phoca barbata*). In one seal (*Halichœrus gryphus*) the tapetal cells are so elongated as to simulate a tapetum fibrosum; but they are still cells, not inert connective-tissue fibers as in a true tapetum fibrosum. The seal tapetum covers a great area of the retina, usually extending at least to the equator of the eyeball in all meridians and often much farther than this on the temporal side, the retinal region which looks ahead of the animal. This record-breaking area of tapetum in the seals will appear significant when we consider its special purpose in these animals (pp. 446-8).

Though the elements of a tapetum cellulosum (unlike those of the true fibrosum type) are living cells, there is not room in them for much protoplasm. They are packed with highly refractive threads or rodlets, in some cases long and with crossings and recrossings to form a feltwork, in other cases very short and set in serried rows so that a 'herringbone' pattern is created (Fig. 93b). These inclusions are formed of some organic substance, perhaps different in different cases, whose chemical nature is unknown; but they appear to be crystalline and homogeneous. In the cat they are yellowish, about 10μ by 0.5–1μ, and

apparently compounded of still smaller elements. Those of the seals have been found to resist weak (but not strong) acetic acid, and are blackened by osmic acid, suggesting a lipoid nature which their double refraction confirms.

Guanin and the Argentea—The best known of the *retinal* tapeta lucida—called pseudo-tapeta by Brücke, who published the first extensive description of tapeta lucida in 1845—are those in which the pigment epithelial cells contain masses of particles, or crystals, of guanin. This substance is also employed in chorioidal tapeta, which otherwise resemble the mammalian tapetum fibrosum. Guanin plays the essential rôle in the amazing tapetum of the elasmobranchs, and it is employed in an altogether different kind of mirror located on the outside of the eyes (and bodies) of fishes. It deserves more than a few words on its own account:

Guanin is chemically a purine, and is closely related to uric acid. In extracted form it is an uninteresting, pale yellow, chalky powder; but when deposited, either as simple guanin or as the calcium salt, in the right places and in the right way, it can endow living tissues with the metallic lustre of silver or gold. Guanin has long been employed, wherever a mirror was needed, by fishes and a few higher vertebrates. Before them, invertebrates had used salts of uric acid to form concentrating mirrors in light-producing organs, which are often built much like an eye. The silvery sides of a minnow are plated with guanin-laden scales. Indeed, the name of the substance comes from 'guano', the term for the excrement (of Peruvian cormorants) which is mined for fertilizer on the sea islands where the piscivorous guanay-birds of millennia once piled it a hundred feet deep. Before it has been through the alimentary canal of a bird, the guanin of fish scales is known commercially as argentine, and under the name of 'essence d'orient' it was formerly used in the manufacture of artificial pearls.

The entire uveal tract of a fish eye becomes jacketed, in the larva, with a guanin-laden outer layer called the argentea. Just as the silver reflections from an adult fish's sides blend with the bright water surface when seen from below by a predator, so does the argentea of a larval fish eye render that eye inconspicuous within the glassy body, by concealing the black pigment of the uvea which has already developed so that the little eye can function. This interpretation of the argentea as an embryonic adaptation to light is confirmed by the fact that it is seldom found in fishes which live in the darkness below 400 meters.

As the fish grows up and the head tissues become opaque, the argentea covering the chorioid loses most of its meaning, though in the enucleated eye it can still be seen shining through the transparent sclera. Where it continues over the face of the iris, however, it has been claimed to serve as a mirror, reflecting light (enough?) toward crannies and crevices into which the fish happens to be trying to look. The head-mirror worn by a physician, which he pulls down so that the hole in it is opposite his eye when he wants to peer down our gullets, might have been copied by its inventor, Czermak, from the argentea layer of a fish's iris. Whether useful in this way or not, the iridic argentea naturally adds to the opacity of the iris (Fig. 67, *a*, p. 159). By reflecting much of the light, the guanin leaves less for the melanin of the rather thin fish iris to absorb.

Guanin in Retinal Tapeta—One of the cleverest uses of guanin is in the retinal tapetum lucidum seen in a few European freshwater fishes and very recently found by George Moore in one of our native species, the pikeperch *Stizostedion vitreum*. Known in *Abramis brama* for about a century, and in *Rutilus rutilus* and *Lucioperca sandra* for decades, this type of tapetum has been described by its chief student, Wunder, also for *Blicca björkna, Pelecus cultratus, Acerina cernua, Lucioperca volgensis,* and (provisionally) for *Abramis ballerus* and *Acerina schrätzer*. Wunder found all of these fishes in Lake Balaton, in western Hungary. Some of them are the most abundant of the 37 species of fishes in that unusual body of water. The 'Balatonsee' is peculiar in that, while enormous in area, it is everywhere shallow—averaging 6 feet in depth; and its waters are turbid almost to the point of opacity for nearly the whole of the year. These tapetum-bearing fishes are quite definitely adapted to this environment, but were of course pre-adapted (see p. 388) before ever they got into it, for most or all of them occur elsewhere in Europe as well. Moreover, the above assemblage of fishes represents at least two separate productions of the same sort of tapetum, for some of the genera (*Abramis, Rutilus, Blicca, Pelecus*) are cyprinid, malacopterygian, fishes; while *Acerina* and *Lucioperca* (the latter a close relative of our *Stizostedion*) belong to the perch family among the Acanthopterygii.

The retinal guanin tapetum may be small, or may form a huge horizontal oval area which practically fills the fundus. It will suffice to describe it for one of the best-known cases, and figure it for another:

In the superior two-thirds of the fundus of *Abramis brama,* a normal amount of fuscin pigment is present in each retinal pigment epithelial

cell. Along with it, partway down the length of the cell-processes, is a cloud of guanin crystals (Fig. 94). The pigment migrates in the usual way, retracting into the body of the cell in the dark and moving far down into the processes in the light (pp. 146, 149). As the fuscin granules surge on their way in either direction, they infiltrate among the guanin crystals, leaving the latter relatively undisturbed in position—indeed, the guanin may migrate to some extent in the opposite direction. Contracting behind the guanin layer in dim light, the pigment exposes the crystals

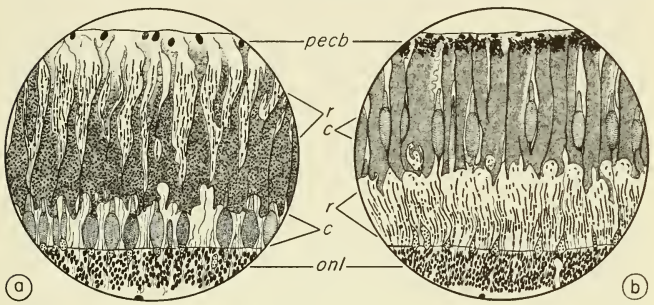

Fig. 94—The occlusible retinal guanin tapetum of certain teleost fishes, as exemplified by the European pikeperch, *Lucioperca sandra*. ×500. Redrawn, modified, after Wunder.

a, visual-cell layer of light-adapted retina, showing cones contracted to limitans, rods elongated, and retinal pigment (black granules) expanded into the heavy pigment-cell processes to mingle with the guanin (silver), destroying its effectiveness as a mirror (*cf.* Figs. 62, 63, 64, pp. 146-8).

b, dark-adapted situation, showing rods contracted toward limitans, cones elongated, and retinal pigment retracted into pigment-cell bodies to expose a guanin mirror distal to the mass of tiny rods.

pecb- pigment epithelial cell bodies; *r*- rods; *c*- cones; *onl*- outer nuclear layer.

to serve as a reflective backing for the mass of rod visual cells. Migrating past the guanin in bright light, into a position between it and the light, the fuscin covers up the guanin layer. No light is then returned through the visual cells, after having once traversed them.

This type of tapetum may be said to be occlusible—that is, capable of being occluded or covered up in bright light when it is not wanted. It is thus fundamentally different (physiologically) from the tapeta of *Evermannella* and other dim-light fishes in which the pigment epithelium is crammed with guanin but contains no migratory dark pigment

with which to cover it up—all of the fuscin being concentrated in small masses in the tips of the pigment-cell processes, as in the sturgeons (*v.i.*).

A retinal (guanin?) tapetum is common in bathypelagic teleosts; and it may be occlusible in the young, which characteristically live much less deeply than the adults, and have both reflective material and fuscin in their pigment cells. The fuscin disappears during growth, so that the adult tapetum is certainly fixed. Like the argentea, the tapetum is lacking in bathybic teleosts which never come near the surface.

The guanin tapetum formed in the pigment epithelium of the crocodiles and their allies is non-occlusible, for the cells contain much guanin and only a little fuscin, which migrates but feebly and is inadequate to blanket the guanin from the light. If we assume that the guanin was put there early in the evolution of the group, before the photomechanical changes dwindled as they have in these reptiles (p. 162), we can imagine that the crocodiles once had an occlusible tapetum but found it unnecessary to maintain it once they had developed an efficient vertical-slit pupil.

Other Retinal Tapeta—Other non-occlusible retinal tapeta are those of the fruit-bats and that seen in the common opossum, *Didelphis virginiana* (but not in *Marmosa,* though all opossums have eyeshine). The opossum structure occupies the superior half of the eye-ground, and is a neat semi-circle with its straight margin running horizontally at the level of the disc (Fig. 93c). The pigment epithelial cells below this level have their normal, dense content of fuscin granules; but in the modified area (Fig. 95) they are twice as tall, devoid of pigment, and packed full of microscopic particles which look like guanin but apparently are not. These granules dissolve readily in histological reagents which guanin resists, and are hence not seen in micrological sections of opossum eyes. The pale yellow particles with which the pigment cells of the fruit-bats are filled are likewise of unknown chemical composition. In the dog, the retinal pigment epithelial cells covering the tapetized part of the chorioid are themselves filled with reagent-resistant reflective particles, which have never yet been accurately studied or described.

Guanin in Chorioidal Tapeta—Guanin also occurs in chorioidal tapeta. That of the sturgeon bears a superficial resemblance to a tapetum cellulosum, with up to twelve layers of cells; but the cells are filled with guanin or a closely related substance (Fig. 96). The pigment epithelium has not been able to rid itself entirely of pigment in the portion which overlies the tapetum. Instead of there being a little pigment in each cell

however (as in a couple of poorly developed ungulate tapeta) there may be none at all in most of the cells. An occasional cell contains considerable pigment in the cell-body (European sturgeons) or a great deal of pigment compactly massed in the tip of a very heavy process (*Acipenser*

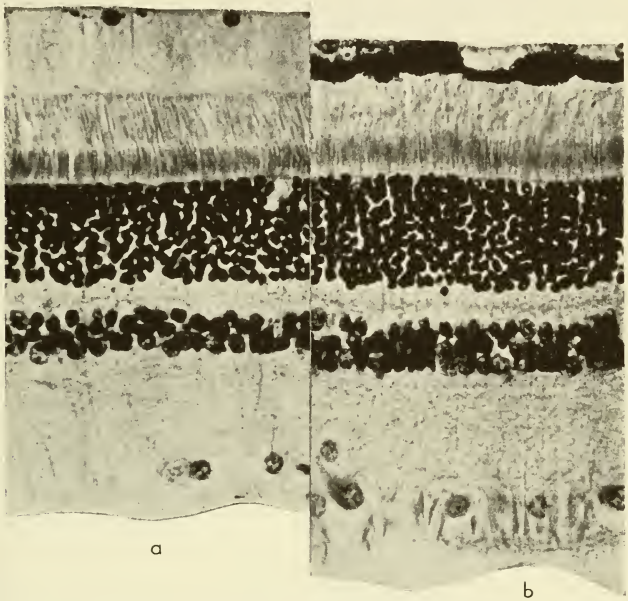

Fig. 95—Retina of the common opossum, *Didelphis virginiana*. ×415. After Walls.

a, from the upper part of the tapetalized region (compare Fig. 93c), showing modification of the pigment epithelium; a very few pigment granules are present, along with a mass of reflective material, in this part of the tapetum (note capillary against external limiting membrane, at right). b, from the inferior fundus, showing unmodified, heavily pigmented pigment epithelium, contrasted with the tapetum in a (*t*) by the alignment of the external limiting membrane in the two photos.

fulvescens—Fig. 96). The effect is as though all the cells had pooled their pigment in a scattered minority of their number, in order to minimize the obscuration of the tapetum. The elements of the tapetum fibrosum in some marine teleosts (most of them bathypelagic) contain large masses of guanin, which were formerly called 'ophthalmoliths'.

TABLE VII—TAPETA LUCIDA

			EYESHINE	CHORIOIDAL TAPETA			RETINAL TAPETA		REMARKS ON TAPETUM
				Fibrosum	Cellulosum	Of Guonin	Occlusible by pigment	Not occlusible	
FISHES	Cyclostomes		−						
	Elasmobranchs		+			+ (occlusible)			Very extensive. Lacking in *Selache*, deep-sea spp.
	Chondrosteans		+ (*Acipenser*)			+			Simulates cellulosum type
	Holosteans, Dipnoans, and Cladistians		*Polypterus* (& others ?)						Character of tapetum unknown
	Teleosts	Many	+						Not known whether a tapetum is present
		Some pelagic marines	+	+					
		Some cyprinids & percids	+				+ (guanin)		(Some freshwater fishes may have tapeta fibrosa)
		Many bathypelagic spp.	+			+		+ (guanin; in *Evermanella*)	
AMPHIBIANS	Anurans	Frogs	−						
		Toads, Hylas	+						
	Urodeles and Cœcilians		−						
REPTILES	*Sphenodon*		?						
	Crocodilians		+					+ (guanin)	
	Turtles		−						
	Lizards		−						
	Snakes		+						Reflex from disc?
BIRDS	Most		−						
	Ostrich, goatsuckers, frogmouths, oil-birds, some owls, etc.		+						Reflex from lamina vitrea?

MAMMALS		Monotremes		?						
	Marsupials	Most		+						
		Didelphis		+						+ (material?)	⌓; filling superior half of eyeground
		Dasyurus, Thylacinus		+	+						In *Petaurus* also?
	Placentals	Insectivores		−							
		Bats	Small	−							
			Flying foxes	+						+ (material?)	
		"Edentates"		+							Trace of fibrosum type in *Orycteropus*
		Rodents	Many	−							
			Many	+							Hystricidae have vivid eyeshine, may have tapetum
			Cuniculus paca	+	+						*Pteromys magnificus* also?
		Lagomorphs		+							
		Carnivores		+		+					△; lacking in *Cynictis* and *Suricata*
		Seals		+		+					Very thick and extensive
		Ungulates and Proboscideans		+	+						⌓; lacking in Suina; weak in *Rhinoceros* & camelids
		Sirenians		−							
		Whales		+	+						⌓; filling superior half of eyeground
		Primates	Lower	+		+					None in *Tarsius*, or *Lemur* (ex. *catta*; here, very thick)
			Higher: *Aotus*	+	+						Most brilliant of tt. fibrosa
			Higher: All others	−							
			Higher: Man	−							Eyeshine as an occasional anomaly

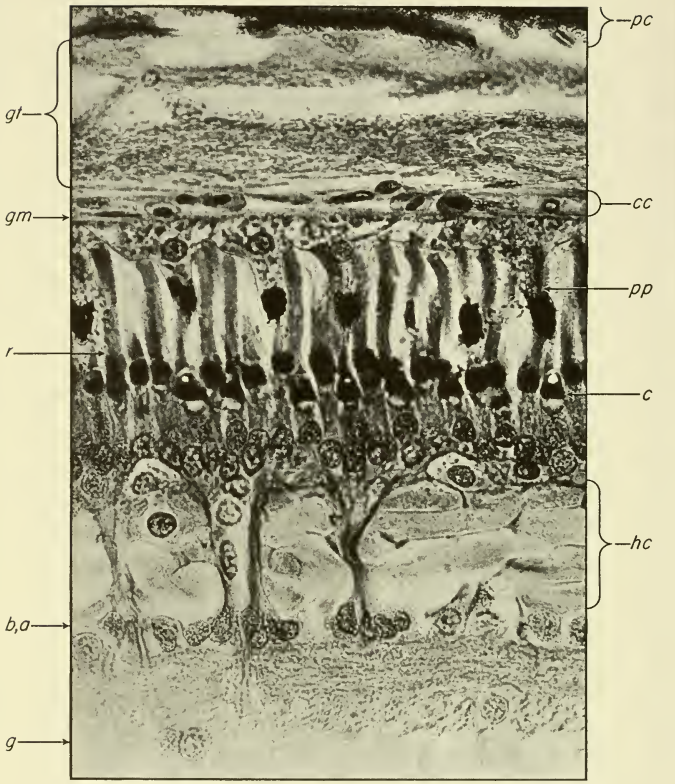

Fig. 96—Retina and tapetum of the rock sturgeon, *Acipenser fulvescens*. × 500.

(The large retinal pigment cells each contain pigment. More commonly, in other sturgeons, the cells are small and only a few contain any pigment).

b, a- bipolar and amacrine cells; *c*- cone (*cf.* Fig. 22a, p. 54); *cc*- choriocapillaris; *g*- ganglion cells; *gm*- glass membrane; *gt*- guanin tapetum, occupying inner portion of chorioid; *hc*- horizontal cells (massive, non-conductive type); *pc*- pigmented portion of chorioid (largely out of the picture); *pp*- pigment-filled process of pigment epithelial cell; *r*- rod.

The guanin tapetum in the elasmobranch chorioid is *occlusible,* and is much the most remarkable of all tapeta lucida despite the fact that its owner is the most primitive living vertebrate type to have a tapetum of any kind. While in other vertebrates the chorioidal pigment cells have at best little ability to change their shape, the elasmobranchs have specialized a layer of such cells whose pigment has extraordinary migratory capacity, in every way equal to that of a teleost retinal pigment cell or a dermal chromatophore. The bodies of these cells form a mosaic toward the inner surface of the chorioid, each with a plate-like process running slantwise (over most of the area of the chorioid) to the choriocapillaris. The processes thus overlap like shingles set at 45° (Fig. 97), and alongside of them are flat guanin-filled cells. In dim light, the migratory pigment retracts into the body of the cell. Light rays which pass through the visual cells and the smooth, pigment-free pigment epithelial cells, now strike the guanin and are thrown back through the visual cells again. In the light, the migratory chorioidal pigment expands so that light rays now strike pigment, instead of the guanin, and are absorbed without reaching the latter. The arrangement works, it is to be noted, only because of the *slanted* position of the alternating plates of guanin and retractible pigment. There is a strip of chorioid, usually horizontal and always superior to the optic disc, in which the guanin plates are not slanted. Here, locally, the tapetum is fixed and non-occlusible. The one known area centralis in selachians—that of *Mustelus* (Fig. 77a, p. 185) —is located within the non-occlusible region. An area centralis (for acuity) and a tapetum (for sensitivity) are of course not incompatible, as is obvious from the situation in the ungulates and carnivores (*v. i.,* and note, p. 185). In at least three elasmobranchs the tapetum is understandably lacking: *Læmargus* is an abyssal shark, *Myliobatis* is a pelagic ray which has cones as well as rods; and the basking shark (*Selache maxima*) basks a good deal, as its name implies.

Phylogeny and Relative Efficiency of Tapeta—One naturally wonders which of these various types of tapeta is most effective; and, if any one is outstanding, why any other types were ever produced. The potentialities of all tapetal types are apparently present in the fishes; but the above questions are quite impossible to answer at present. It seems surprising that so ingenious a device as the elasmobranch tapetum should not have persisted all the way to the mammals—or at least have been re-invented one or more times. But it must be remembered that diurnality

and nocturnality come and go in evolution as mutatory capacity and ecological expedient direct. Each return to diurnality in a given line of descent will abolish any pre-existing tapetum. Upon a subsequent swing toward nocturnality, the group starts from scratch and is as likely to hit upon one device as another, where so many solutions to the same problem are possible. In no other way can we account for the spotty

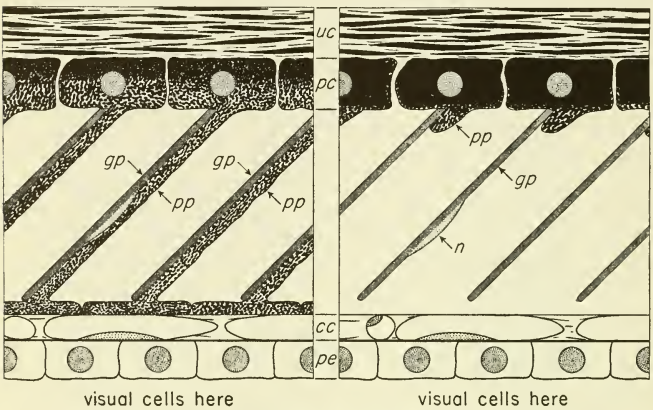

Fig. 97—The occlusible chorioidal guanin tapetum of the elasmobranch fishes. Semi-diagrams based upon *Mustelus mustelus* as figured by Franz.

The guanin is shown in silver. At the left: sagittal section through the chorioid of a light-adapted eye, showing pigmented processes expanded over the proximal surfaces of the guanin plates, shielding them from the light which has passed through the retina. At the right: dark-adapted condition, showing pigmented processes retracted to allow the guanin to reflect light back through the visual cells.

cc- choriocapillaris; *gp, gp*- guanin plates; *n*- nucleus of guanin cell; *pc*- layer of migratory chorioidal pigment cells; *pe*- pigment epithelium of retina (devoid of pigment); *pp, pp*- pigmented processes which can be advanced and withdrawn; *uc*- unmodified portion of chorioid (largely out of the picture above; shows ordinary flat, static pigment cells).

distribution of tapeta as such, and of each type thereof. Only in the Carnivora-Pinnipedia is it likely that a pair of large taxonomic groups share a tapetal type in common by virtue of inheritance from a common ancestor.

At present, no one can arrange tapeta in any order with respect to their reflection coefficients, their efficiency as mirrors. Apart from the manifest superiority of occlusibility, there is only one factor in whose

variations we can see an obvious effect upon tapetal efficacy. This is the distance of the reflective material from the tips of the visual cells. Where this distance is greater, as in chorioidal tapeta (separated from the tips of the rods by the thickness of the choriocapillaris and the pigment epithelium), the spreading of the scattered reflected light results in its striking many rods in addition to those which it had originally traversed before reflection. Where the tapetum smoothly and directly contacts the visual-cell palisade, as in the opossum, there is less opportunity for scattering to blur the image and detract from the acuity of scotopic vision—low, at best, as it is bound to be. Yet the opossum gives every evidence of having extremely low visual acuity, while the cat is far from being badly off in this respect (see Table V, p. 207). If there were anything logical about the distribution of tapetal types, the cat would have the opossum's, and the opossum, the cat's.

The Tapetum and Visual Acuity—The tapetum is not always restricted in usefulness to the dimmest of illuminations. As was pointed out in Chapter 7, the all-round capacity of twenty-four-hour eyes is not due to a fence-straddling avoidance of specialization, but to a mosaic of compatible specializations for both scotopic and photopic vision. A tapetum is perfectly compatible with an area centralis (though it is never associated with a fovea). *Mustelus* is matched, among the primates, by *Lemur catta* and *Aotus*. One of these is diurnal, the other nocturnal; but each has both an afoveate area centralis and a tapetum, while the close relatives of both (other *Lemur* spp., other Simiæ) have neither of these features.

Notably, the ungulates and some carnivores (lion, polar bear) have large eyes but not particularly small images. They can compensate for the dimness of the large image by means of the tapetum, the size of the image enabling them to attain keen vision despite the low ratio of cones to rods. In dim light the tapetum gives the animal enough sensitivity, and in average light it is still usable because of the size of the image. It is certainly not ordinarily a source of dazzlement as is evidenced by the fact that few ungulates and no large carnivores have any approach to a slit pupil. It is probably no accident that in these animals the area centralis falls within the confines of the tapetum. If cones are indeed concentrated within these imperfectly known areæ centrales, the lowered sensitivity of those regions is nicely compensated by the tapeta behind them.

We do know that the visual acuity of ungulates is far higher than we would expect to find in the average tapetum-bearing *nocturnal* animal with its rod-rich retina—the average dog-sized carnivore, for example—despite the rather large absolute size of the eyes of foxes, cats, and the like. The old-time Arab horse breeders are said to have invented a game in which the winner was he whose horse recognized him, from upwind, from the greatest distance—showing its recognition by heading straight for its master who stood with the other owners in a great semi-circle at a considerable distance. The champion seems to have been a horse which recognized his master from 500 meters away. And the vision of the horse is superb by night as well as by day. An Arabian fable cited by Rochon-Duvigneaud runs like this: "The Lion and the Horse were arguing as to which had the better vision. The Lion, on a dark night, could see a white pearl in milk—but the Horse could see a black pearl amidst coal. The judges decided in favor of the Horse."

Another empirical example, which could hardly be improved upon, is that given in the observations made by an old hunter on the prong-horn (*Antilocapra americana*), and quoted by Seton: "What a live antelope don't see between dawn and dark, isn't visible from his stand-point; and while you're a-gawkin' at him through that 'ere glass to make out whether he's a rock or a goat, he's a-countin' your cartridges and fixin's, and makin' up his mind which way he'll scoot when you dis-appear in the draw for to sneak on 'im—and don't you ferget it."

Chapter 10

ADAPTATIONS TO SPACE AND MOTION

(A) Accommodation and its Substitutes

Any object in visual space may have a number of perceptible attributes: size, shape, pattern, brightness, color, position, motion, and distance. Our awareness of most of these derives fairly directly from the character of the retinal image itself, whose size and shape, tempered by experience and memory, tell us the 'true' size and shape of the object. We translate subjective luminosity into objective intensity, making unconscious allowances for our adaptation-condition and for the illumination of the moment. A white object thus seems white even when it is reflecting less light than some black object seen under other conditions. So also with color, which remains remarkably constant in our minds even though the illumination be qualitatively altered. Pattern resolves into variations of brightness and color, motion into a varying stimulation of successive retinal regions.

Dependence of Apparent Distance upon Size—When we consider distance however, we are dealing with an object-attribute concerning which the retinal image, alone, can give us no information whatever. A light ray is a straight line, and when one end of that line lies in a visual cell the physiological result is the same no matter how near or how far the other end of the line may be. For our knowledge of the distance of a visual object, we are much more dependent upon past experience than upon what our eyes can tell us at the time.

To know either the size or the distance of an object, we must know the other. If we do not know one of these facts, we do not know either. The farther an object is, the smaller its retinal image and the smaller its apparent size. If it looks small and we know it to be large, we judge it to be far away. If it looks large and we know it to be small, we judge it to be close at hand. Brightness, haziness, overlapping of other objects, perspective, vertical position with respect to the horizon, and parallax are other factors in monocular judgement of distance; but like size itself, most of these are in a sense interchangeable with distance and can aid us to accurate estimations of distance only in so far as they themselves are

accurately evaluated. Thus, strangers in mountainous country underestimate distance because of the exceptional clearness of the air—in their experience, objects look that sharp only when they are nearer. Similarly, distances through mist and fog are easily overestimated, since ordinarily such hazy outlines and unsaturated colors connote greater distances.

An amusing and convincing demonstration of this interdependence of size- and distance-judgements is the following experiment, which the reader can make without travelling to the Rockies or waiting for a fog: Stand before a large mirror with arm outstretched before you, index finger pointing upward. Watching the finger closely, move it toward you and away from you, noticing your reflection in the mirror all the while but without taking your attention off of your finger. As the finger approaches your face, your image in the mirror will appear to shrink and recede; and when the finger is moved toward the mirror your reflection will seem to advance and expand.*

The point is that judgement of distance is very largely subjective and is very easily deceived. This, despite the fact that the eye may make a thoroughly objective and very precise adjustment to the distance of the object to which we are giving attention, the adjustment called accommodation. If nature has anywhere fallen down very badly in designing our visual mechanism, it is in neglecting to tie our awareness of distance firmly to our neuromuscular apparatus for adjusting to it, which would have put the estimation of distance upon an objective basis. However, nature may be pardoned on this score so far as we humans are concerned, for we have binocular vision at a maximum and gain a potent cue to distance, from the convergence which our eyes automatically perform along with their accommodation, and which takes place even beyond the limit of distance within which accommodation is necessary for most of us.

It is not distance as such, or its variation as such, that makes accommodation necessary. Some animals get along nicely without it, even though they may be standing alongside of others which are utterly dependent upon accommodation for maintaining an equally sharp image of an object at which both are looking. The need for accommodation, or

*Explanation: As the finger nears your face its retinal image enlarges; but since your attention is steadily upon the finger, which is very familiar to you and whose size you know to be constant, you see it as having the same size as ever. By contrast, however, the motionless image of your whole body, over which the finger is superimposed, becomes relatively smaller and is hence perceived as shrinking in size. And, since in your experience decreasing (or apparently decreasing) size always means increasing distance, your image seems to recede farther behind the mirror. As the finger is moved away these processes are reversed and the mirror image apparently enlarges and comes toward you.

the lack of need, resides in the plan of the eye itself and not in the distance of the object.

The Why of Accommodation—The ideal human eye, in a state of internal rest, is said to be emmetropic. By this is meant that parallel rays of light, striking the cornea through air, are brought to a point focus on the retina (Fig. 12, p. 27). It needs to be emphasized that the *average* human eye is not emmetropic. Emmetropia is decidedly the exception, not the rule. The most prominent student of mammalian refraction, Lindsay Johnson, found a slight and beneficial degree of hypermetropia in the eyes of primitive peoples, and considered that this might be the truly *normal* human situation.

In emmetropia, if we should gaze at the sun for a long moment, a tiny hole would be burned through the retina in the region of the fovea—the focus of those intolerably intense, parallel rays. If we set up an experimental source of milder parallel rays in a dark-room, it can be at any distance beyond twenty feet and will theoretically always have the same brightness, for the same sized light-pencil (just filling the pupil) will be brought to a point focus.

But natural objects are not giving off parallelized beams of light. From each point on the object, rays diverge away in many directions and only a few of them are aimed at the pupil of a nearby eye. Unless these are brought to a point focus in the layer of visual-cell outer segments, we will not see that object-point as a point and cannot build up a sharp retinal image of the object (Fig. 10, p. 25). The light by means of which we see the object-point is thus a cone, its apex the object-point and its base the pupil—or more accurately, that circle of cornea from the circumference of which rays bent by the corneal surface can just enter the pupil.

As the object approaches, the cone of light entering the eye from each point on it becomes a shorter, stubbier cone with a much greater angle at the apex, so that more of the light rays emanating from each point are now caught by the pupil and the object looks brighter. But these rays are now striking the corneal surface at lesser angles than before and if the ray-bending (focusing) power of the eye remains unchanged, the point at which they are brought together will move backward in the eye and slip off the tips of the visual cells into insensitive pigment epithelium. The eyeball being then too short, its vision becomes like that of a hypermetropic or far-sighted eye (Fig. 12), and the visual cells register only blur-circles. To bring the crisp image forward into the visual-cell layer

again, either the optical center of the eye must be moved forward, farther from the retina, or else the ray-bending power of the dioptric apparatus must be increased—by sharpening the curvature of the lens, the cornea, or both.

Both of these general methods of accommodation—by moving the lens (Figs. 98 and 99) or by increasing its curvature (Fig. 100)—are in use among various vertebrates. Through evolution, there has been a tendency to abandon the first method for the second, simply because of greater ease of making it mechanically precise and positive, rather than because of any inherent optical superiority of the one method over the other.

Accommodation is necessary, then, to keep a sharp image of an approaching or receding object within the thickness of the visual-cell layer. The word as used by medical men refers only to the adjustment for approach or static nearness, but this application is hardly broad enough for our purposes; for, in some vertebrates, the resting eye is myopic, making a saving of muscular effort since the eye is used mostly at close range. Parallel rays are then focused in front of the retina, and the lens must be moved backward to adjust for a distant object—a 'negative' accommodation as compared with our own (Fig. 98).

Obviously, the need for accommodation depends upon two things: the amount of forward or backward shift of the image relative to a given shift of the object, and the length of the visual cells. When an emmetropic human eye fixates an object at the horizon, its image falls somewhere in the layer of outer segments—presumably very close to their inner ends. Now, that object can approach the emmetropic eye to a distance of only twenty feet without its image moving backward a distance greater than the length of the outer segments—a tiny fraction of a millimeter. The approach of the object is thus minified far more than are any sidewise movements it may make. The image moves backward faster and faster, however, as the object comes up; and when it comes within twenty feet the lens must begin to sharpen its curvature to keep the optical image coinciding with the photochemical image in the outer segment layer. When we have sharpened the curvature of the lens as much as we can, and the object is still clearly seen, it is said to be at our 'near point'—which may be a few inches before our eyes if we are young, or beyond comfortable arm's reach if we are middle-aged and 'presbyopic.' When we are very old and the lens is too hard to deform at all, the near point has of course receded from us to the twenty-foot distance (Fig. 15, p. 35).

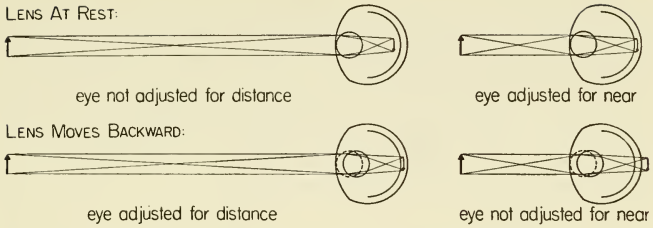

Fig. 98—The 'negative' accommodation of those animals whose effort of accommodation moves the lens backward (lampreys; teleosts; probably holosteans).

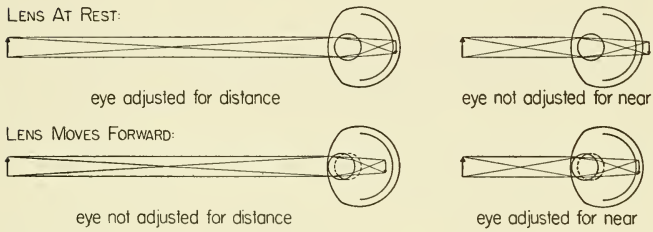

Fig. 99—The 'positive' accommodation of those animals whose effort of accommodation moves the lens forward (elasmobranchs; amphibians; snakes).

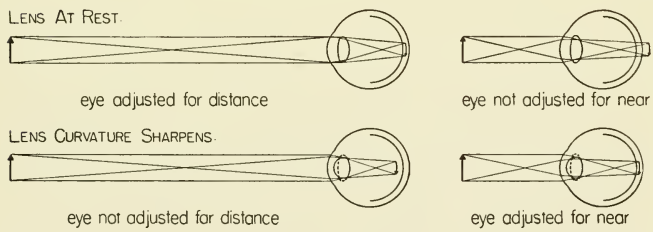

Fig. 100—The 'positive' accommodation of those animals whose effort of accommodation sharpens the curvature of the lens (reptiles except snakes; birds; mammals).

There is nothing mystical about this twenty-foot distance. It *is* that distance because of the size and structure of the human eye and the length of human visual cells. This is most important to remember; for there is a naïve tendency for some to assume, on learning that some animals have no accommodation, that those animals must have hazy images of all objects nearer to them than twenty feet. This is not true—the twenty-foot distance is just as much a part of the human eye, and only of the human eye, as its diameter or its weight.

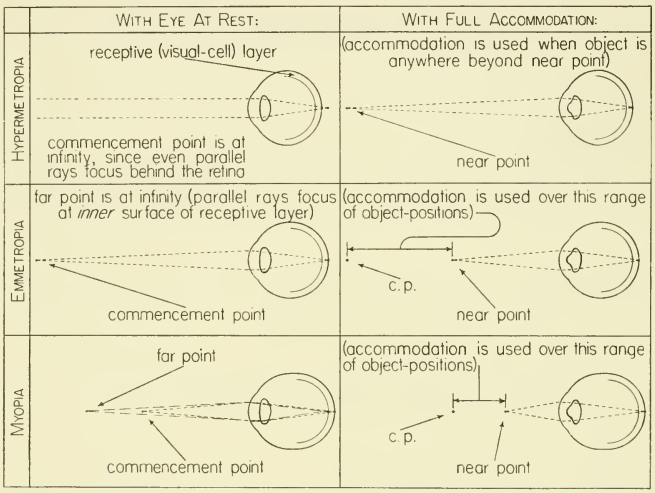

Fig. 101—Object-positions in relation to accommodation and refractive errors.

The greatest distance at which an object can stand from an eye, and still be sharply imaged on the retina, is called that eye's 'far point'. Suppose we call by the name 'commencement point' that least distance an object can have without there being any necessity of accommodation. For the emmetropic human eye, then, the commencement point—the point, in the approach of the object, at which the eye must begin to exert accommodatory effort—is around twenty feet. The hypermetropic or far-sighted human eye has a much more distant commencement point. Theo-

retically, it lies at infinite distance, for such an eye must accommodate to some extent to bring even parallel rays (theoretically hailing from infinity), let alone rays which diverge ever so slightly, to a focus on the retina (Fig. 101). The near point of a far-sighted eye is likewise farther away than that of an emmetropic eye. In myopia the near point is very close, and the far and commencement points coincide.

But hypermetropia and myopia are abnormalities in human eyes only because human visual requirements are best met by what we call the 'normal' condition of emmetropia. We walk and run fast enough to require sharp vision, without the expense of intraocular muscular exertion, for distances greater than twenty feet ahead of us. If we habitually travelled faster—as we are coming to do in this motor age—we should not need a more distant commencement point, since by relaxing our accommodation we can see sharply as far ahead as the clarity of the atmosphere allows. But if we habitually crawled on our bellies, we would be much better off with a closer commencement point, else we should constantly be exerting accommodation for the distances we most needed to be able to see ahead. Civilized men are so dependent upon clear images of things which they manipulate with their hands that they need a fairly close near point. If we were all engravers, we would be better off with a still closer one—and the 'normal' human eye would be a *myopic* one.

That the human eye, ideally, is emmetropic is thus a mere coincidence, and not a *sine qua non* for all animal eyes. Naturally, there are many animals with diverse habits which make them need farther or closer commencement points and near points than ours. It is absurd to call their eyes inferior or disharmonious simply because they do not happen to be emmetropic.

Devices Which Make Accommodation Unnecessary—We have seen in earlier chapters that most of the advantages in vision seem to be on the side of large eyes as against smaller ones. Here, with the matter of accommodation, the shoe is on the other foot. In a small animal with small eyes which, *ceteris paribus,* looks customarily at small objects, the retinal image not only shifts less laterally when the object moves sidewise in the opposite direction, but recedes less within the retinal thickness when the object approaches. Consequently such an eye has a much closer commencement-point than a large eye—it need not begin to accommodate until the object is much nearer. Not only that, but the visual cells are no smaller in small eyes—just as they are no larger in large eyes,

which the reader will remember as the chief reason why large eyes afford better-resolved cerebral images (see p. 171). Consequently a small object can come very close to a small eye before its image recedes off the tips of the visual cells—as close, perhaps, as the near-point of a large eye possessing a good mechanism of accommodation. On top of all this, the small lenses of small eyes have much greater 'depth of focus' than do the lenses of large eyes; for, the shorter the focal length, the greater the depth of focus of a lens. The result may well be that the small eye needs no accommodation at all—so, when we find that the mechanism of accommodation has undergone phylogenetic atrophy in many small-eyed nocturnal mammals we are hardly justified in mournfully shaking our heads at their 'degeneracy'.

In eyes which are large enough to seem to require a capacity for accommodation, there are still four ways to dodge the demand and obtain clear images of objects at various distances, successively or simultaneously, with a perfectly static intra-ocular situation. All four of these substitutes for accommodation have been devised and successfully employed by different vertebrate animals. They are:

1. An increase in the length, or the effective length, of the visual cells. Vertebrates are strictly limited in the actual lengthening of the receptor elements, for any such elongation increases the distance between the inner layers of the retina and an important source of their supplies, the choriocapillaris. If carried to extremes, this would be detrimental to retinal nutrition. The cephalopod molluscs with their erect retinæ are under no such handicap, and the visual elements of a squid are so enormously long that the image can recede and advance through their length, corresponding to great excursions of the object to and from the eye, without making any demands upon the inefficient apparatus of accommodation. Where vertebrates have very long visual cells, as in deep-sea fishes and some geckoes (see Fig. 25, p. 62), it is of course primarily for the sake of increasing their sensitivity, though as an incidental effect it partially obviates accommodation. But in the great fruit-bats, the so-called flying foxes (Macrochiroptera), a unique alteration has resulted in a great increase in the effective length of the rods without these cells being actually elongated at all: the chorioid is beset with innumerable conical eminences which deform the visual-cell layer, the elements of the latter being set endwise against the chorioidal papillæ like the trees in a range of mountains (Fig. 102a). Thus no matter how near or far the object may be, its image falls sharply upon a set of rods standing at a

corresponding level on the sides of the chorioidal mountains. Presumably the bat sees the visual field at a given distance as a (relatively!) sharp reticulum, the lacunæ of the lace-work being much more badly blurred. The small bats (Microchiroptera) do not have this device, but they are not at all dependent upon their vision, which is very poor; and their eyes are so tiny anyway as to need no accommodation or substitute therefor.

2. A tilted attitude of the retinal surface relative to the visual axis of the eye. This is the equivalent of slanting the plate of a camera so as to have, in simultaneous sharp focus, objects at different distances—as is done for example in photographing tall buildings from the ground. In some invertebrate eyes the retina is built like a flight of steps. Among vertebrates the rays and the horse (and probably many other, unstudied

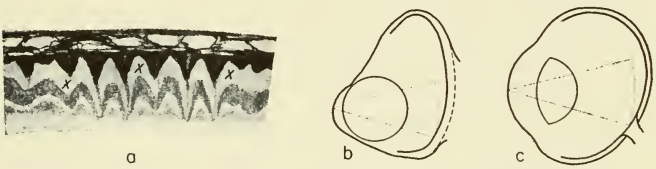

Fig. 102—Two devices which make accommodation unnecessary.

a, retina and chorioid of a fruit-bat, *Pteropus medius*, showing chorioidal mammillation which places the visual cells at many different levels. x 48. After Kolmer. *x, x*- visual-cell layer. b, eye of a ray, *Raja batis*, in vertical section, showing how retina forms a 'ramp'—the axial length of the eyeball changes continuously in the vertical meridian. Based on a drawing of Franz. c, eye of horse in vertical section, showing ramp retina. Redrawn from Nicolas.

ungulates) appear to have produced a similar device, using a ramp rather than a stairway. The retina is progressively farther from the lens superiorly than it is inferiorly (Fig. 102b, c). The horse, which has no power of accommodation, apparently has only to tilt the eye slightly up or down to have a sharp retinal image of any object over a considerable range of distance. This is however only a suspicion which awaits experimental justification.

3. The use of a stenopaic aperture. This, which is simply a single or multiple pin-hole pupil or a device which gives the effect of one (as in the seals—see p. 447), has the virtue of producing a pretty sharp image regardless of the distances from it to the object and the retina. In fact, we may fairly say that the vertebrates brought the need of accommodation upon themselves, in the first place, when they adopted the lens as a

means of forming an image upon the retina, instead of the pinhole as *Nautilus* (Fig. 1d, p. 3) chose to do. As Figure 89 (p. 224) shows, the pinhole is a much simpler gadget than the lens, and the image it forms is quite sharp when caught on a screen at any reasonable distance. But it has one very great disadvantage: the amount of light, emanating from an object-point, which can form a corresponding image-point, is just the slender pencil of rays which get through the pinhole. Apparently, this pencil should be a single ray if the image is to be maximally sharp, and the size of the pinhole would then be a quite impractical, mathematical point.

Actually however, as the pinhole is made smaller and smaller, the image at first sharpens but finally becomes more and more blurred through the introduction of diffraction. The optimal diameter of a pinhole aperture is equal to twice the square root of the product of the screen-distance and the wavelength of the light. An ideal pinhole located, say, at the position of the inner surface of the cornea in a lensless human eye, would need to be 0.23 millimeters in diameter; and a point four inches from the eye would then be imaged on the retina as a one-millimeter circle.

A lens gathers in a *cone* of light-rays from each point of the object, and converges all of this light again to form a point in the image, which is hence far brighter than the one formed by a stenopaic aperture. Other things being equal, the broader the lens, the brighter the image. Where a pinhole is employed to eliminate the need for accommodation at certain times or all the time, the retina must be very sensitive even though the stenopaic aperture is used in bright light. A reduction of the need for accommodation—what a photographer would call a deepening of the focus of the eye—is an incidental gain of any slit-pupilled animal; for a slit, like a round pinhole, is to be considered a stenopaic aperture, although an astigmatic one. And, slit-pupilled vertebrates always have the necessary extra sensitivity in their retinæ to make vision remain bright enough when the slit is closed down. That is why they *have* the slit.

Animals whose pupils are specially designed to provide stenopaic apertures include *Scylliorhinus* (Fig. 91, p. 225), *Raja* (Fig. 65, p. 158), geckoes (Fig. 88, p. 223; and see p. 224), some ungulates (especially camelids—Fig. 86c, p. 219), the domestic cat, and *Paradoxurus*. Still others have the benefit of a pinhole in bright light, though their phenomenally contractile circular pupils are no doubt intended primarily to shield an extra-sensitive retina—a job which ordinarily calls for a slit

pupil. These animals are *Encheliophis,* the sea-snakes, *Tarsius, Pedetes,* and the two-toed sloth (see Table VIII, pp. 272-3).

4. The employment of two separate visual mechanisms which are permanently set for two particularly useful distances. This method is very common among the arthropods, where it is expressed in the combination of compound eyes and simple ocelli as seen in the average insect. Among the vertebrates, it is used only in the tubular eyes of deep-sea fishes, whose lenses are relatively so enormous that adjusting them very much is quite out of the question. Here there is often a second (sometimes even a third) 'accessory' retina far up the side of the eye, close to the lens (Fig. 136, p. 400). Distant objects can be seen with this retina while nearby ones are imaged farther from the lens, on the orthodox retina at the bottom of the eye. The effect of this arrangement is essentially like that of the bifocal spectacles to which we resign ourselves in presbyopia. An even closer approach to a literal bifocal lens is seen in the kingfishers and particularly in the famous 'four-eyed fish' *Anableps,* though with different significances (see pp. 434-5 and 442).

Vertebrate Methods of Accommodation—Few eye-minded vertebrates have eyes small enough to get along without accommodating, or have produced one of the four substitute devices described above. The vast majority alter the optical system dynamically, either by pushing or pulling the lens backward (Fig. 98) or forward (Fig. 99)—the group of methods employed by all of the Ichthyopsida (fishes and amphibians); or by changing the shape of the lens (Fig. 100). This may be accomplished:

A. By squeezing the lens at its equator positively and vigorously by means of the ciliary body, and with the sphincter of the iris sometimes called into play to help deform the anterior surface of the lens. This method is used by all of the Sauropsida (reptiles and birds) except the snakes, whose ancestors lost the mechanism during their early ocular degeneracy. The snakes have evolved, as a substitute, a version of the ichthyopsidan method which is all their own.

B. By relaxing, through muscular effort, a tension which normally exists (when the muscles are at rest) in the fibers of the suspensory ligament of the lens—thus allowing the elasticity of the lens capsule to mold the soft lens cortex into a new form with a sharper curvature. This is the method of the Mammalia (and man), and differs considerably from the ancestral sauropsidan one because of the disappearance, in the early mammals, of some structures essential to the complete sauropsidan mechanism.

These three kinds of intra-ocular movements are nearly always accomplished entirely by intra-ocular muscles. Extra-ocular ones have been suspected in some cases of helping to alter the lens-retina distance by deforming the eyeball in a regular manner. The mechanisms involved are described below, and are summarized in Table VIII (pp. 272-3), which should be consulted during the reading of the remainder of this Section.

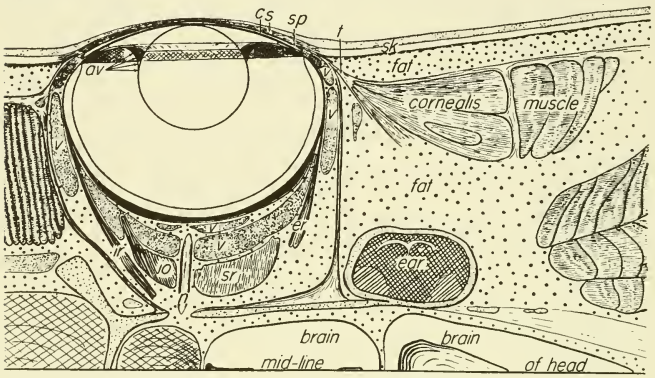

Fig. 103—The eye and surrounding structures in a lamprey, *Lampetra fluviatilis*, in horizontal section; the anterior end of the animal is to the left. Modified from Franz.

av- anterior surface of vitreous; *c*- cornea; *er*- external rectus; *io*- inferior oblique; *ir*- internal rectus; *n*- optic nerve; *s*- spectacle (a 'window' in the head skin); *sk*- skin; *sp*- space between spectacle and cornea; *sr*- superior rectus; *t*- tendon of cornealis muscle, inserting into spectacle; *v, v*- venous sinuses which cushion eyeball.

Lampreys—Inserted into the rim of the primary spectacle (see p. 449*f*) at one side is the tendon of a massive muscle (Fig. 103) which lies in the head outside of the orbital capsule and caudad from the eye, and represents portions of two myotomes. When this 'musculus cornealis' is contracted, the spectacle is drawn taut and flattens the cornea. Since the lens touches the latter on the inside, it is pressed backward and nearer to the retina. The near-point of the resting eye is very close—about five inches, for the eye is eight diopters myopic. In accommodation the eye of course becomes emmetropic and may go on into a fairly high degree of hypermetropia.

Accommodation in the cyclostomes is thus accomplished by deforming the eyeball from outside. The return to the resting shape is effected

through the elasticity of the sclera and vitreous and the equality of intra-ocular pressure throughout the globe. This method is at the mercy of quick, great changes of hydrostatic pressure and so would not work well in a fish which makes rapid changes in the depth at which it swims. Despite the manipulation of the eyeball by the muscle or by water pressure, the lens cannot become dislocated, for it projects well through the pupil and is firmly held fore and aft by contact with the cornea and the vitreous (Fig. 103, *av*). There is no zonule or suspensory ligament, nor any need of one, for the spherical lens is trapped like one of the balls in a ball bearing, the pupil comparing with the aperture in the ball cage and the cornea and vitreous acting like the outer and inner races.

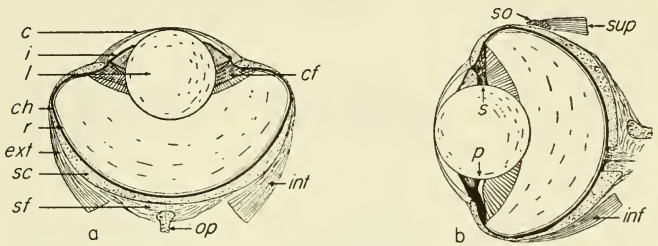

Fig. 104—The elasmobranch eye and its mechanism of accommodation—*Carcharodon carcharius*. × 1⅓. Combined from figures of Franz.

The eye is represented in full accommodation; were the protractor lentis muscle relaxed, the lens would be withdrawn from the cornea. a, horizontal section. b, vertical section.

c- cornea; *ch*- chorioid; *cf*- ciliary folds, from which gelatinous zonule passes to lens equator; *ext*- external rectus; *i*- iris; *inf*- inferior rectus; *int*- internal rectus; *l*- lens; *op*- optic pedicel; *p*- papilla bearing protractor lentis muscle; *r*- retina; *s*- suspensory 'ligament' (a thickening in the zonule); *sc*- scleral cartilage; *sf*- fibrous portion of sclera; *so*- superior oblique; *sup*- superior rectus.

The musculus cornealis does not interfere with the rotation of the eyeball, as it would do if inserted into the true cornea instead of into the primary spectacle. There is obviously some reason to think that the conversion of the spectacle into a conjunctiva (see Chapter 11, section D) had to wait for the evolution of intra-ocular muscles of accommodation. It has been claimed that the lamprey's oculomotor muscles (which are very thin and much blended where they cling to the globe, and reach far forward so as to form a smooth jacket) accomplish accommodation for near objects by contracting in unison and thus elongating the eyeball. There is as yet no adequate experimental basis for this belief, and

there would seem to be no need whatever for such an action since the resting eye is too long (that is, myopic) to begin with. Such an action of the external muscles might however serve to combat any temporary flattening effect of water pressure in lampreys which descend to considerable depths, as ocean species are known to do.

Elasmobranchs—In the elasmobranchs the lens is again spherical or nearly so (Fig. 104). The iris does not commence at the ora terminalis as in lampreys, for a ciliary body with many low radial folds intervenes. A washer-shaped, gelatinous membrane, attached peripherally over the whole surface of the ciliary body and centrally around a narrow equatorial zone on the lens surface, serves as a zonule. A dorsal, radial thickening in this membrane gives the lens most of its actual support. Diametrically opposite, in the ventral meridian, there is an elaborate papilla on the ciliary body which contains smooth muscle fibers. These fibers are so oriented that when they contract, they swing the lens pendulum-fashion toward the cornea. Accommodatory effort is thus exerted for near vision, as in ourselves, and not for distant vision as in lampreys and teleosts. The anterior chamber is very shallow, but there is always some space between the relaxed lens and the cornea. The depth of this space represents the range of accommodatory movement of which the lens is capable—unless, as may be, the little protractor lentis muscle is strong enough to make the lens bulge the cornea somewhat. The eyes of elasmobranchs have considerable hypermetropia—ten to fifteen diopters in various species, according to Franz; but they can accommodate from fifteen to twenty diopters, hence may have very close near points.

Teleosts—Teleost fishes have a mechanism which is superficially similar to that of the elasmobranchs but actually can have no evolutionary connection therewith. Here again the lens is spherical, and touches the cornea as in the lampreys (Fig. 105). It is suspended by a dorso-nasal ligament consisting of material essentially like tough vitreous, and running from the pars cæca retinæ to the surface of the lens a little anterior to its equator. On this ligament the lens can swing—not freely as an undamped pendulum however, since there is evidence for the presence of a diaphanous zonule with radial and even circular fibers, anchoring the lens to the pars cæca in all meridians.

Approximately diametrically opposite the suspensory ligament, but with much variation in location and structure from species to species, is the tendinous insertion, in front of the lens equator, of a small ecto-

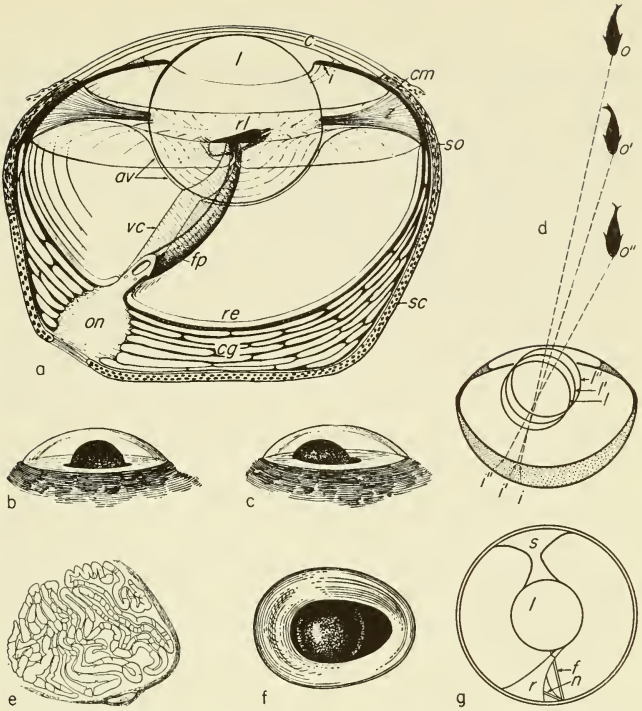

Fig. 105—The teleost eye and its accommodation.

In each drawing (except **e**), the temporal side of the eye is on the left, the nasal on the right.

a, generalized teleost eye in horizontal optical section. After Franz. *av-* anterior surface of vitreous; *c-* cornea (*cf.* Fig. 67, p. 159, for detailed labelling of its three portions); *cg-* chorioid 'gland'; *cm-* ciliary muscle (tensor chorioideæ'); *fp-* falciform process; *i-* iris; *l-* lens; *on-* optic nerve; *re-* retina; *rl-* retractor lentis muscle; *sc-* scleral cartilage; *so-* scleral ossicle (*cf.* Fig. 130b, p. 380); *vc-* vitreous cleft; *z-* zonule. **b**, left eye of *Blennius sanguinolentis* from above, in relaxation. ×3. After Beer. **c**, same as **b**; in full accommodation; note temporad duction of lens accompanying retraction. **d**, the adjustment of a teleost eye for an approaching object (relaxation of the retractor muscle, and return of lens forward to its rest position); *o-o'-o''-* successive positions of object; *l-l'-l''-* successive positions of relaxing lens; *i-i'-i''-* successive locations of retinal image, in the absence of a fovea which would call for fixative rotation of the eye. **e**, cross section of optic nerve of *Serranus cabrilla*, showing edgewise-folded ribbon structure characteristic of many teleosts. From Franz, after Studnička. **f**, eye of *Serranus cabrilla* in relaxation, showing anterior aphakic space common in teleosts and often associated with a fovea temporalis. Modified from Beer. **g**, diagrammatic frontal section of teleost eye, showing mechanism of accommodation. Based on a figure of Meader. *f-* embryonic fissure; *l-* lens; *n-* motor nerve in falciform process; *r-* retractor lentis muscle; *s-* suspensory ligament.

dermal retractor lentis muscle, sometimes called the 'campanula (or plumula) Halleri'. The other tendon of this muscle originates temporally and cranially in the anterior end of the falciform (= sickle-shaped) process where such is present. The falciform process is a ridge in the floor of the eyeball, running from behind and temporally (near, at, or even from above the disc) forward and nasally along more or less of the length of the original course of the embryonic fissure of the optic cup (see Chapter 5, section A). The falciform process may be most simply (though not too accurately) described as a herniation of the chorioid up through the unclosed fissure. It is lacking in many fishes without much regard to their taxonomic positions, and its place in the internal nutritional system of the eye is always taken by a system of ('hyaloid') blood vessels spread out in a thin membrane at the vitreo-retinal interface. In fishes which lack the falciform process, the lens-muscle is kept but its fixed anchorage punctures the retina near the ora.

The nasoventral attachment of the lens-muscle, and its orientation, result in a backward (craniad) and temporad duction of the lens upon contraction. The impulses to contraction come over a large branch of the oculomotor nerve which runs along through the chorioid beneath the falciform process and, accompanied by a blood vessel, departs from the process anteriorly and runs free through the ocular cavity to reach the little muscle. The movement of the lens is roughly opposite to that accomplished in the elasmobranch eye by the protractor lentis, and accommodates the teleost eye for distance instead of for near.

Except in the tubular eyes of many deep-sea teleosts (whose lenses can only be moved slightly backward, if at all), the lens moves laterally, toward the fish's tail, rather more than it moves backward into the retinal cup. This is particularly true in species which have a fovea (see p. 304). During accommodation, a teleost's attention is obviously upon the image in the temporad periphery, which is the location of the area centralis and is the part of the retina involved in binocular vision.

The retractor lentis muscle in its various manifestations undoubtedly does all of the actual work of accommodation in the teleost eye. However, in this group a ciliary muscle is first seen. It is so very small that it makes no bulge in the ciliary region of the uveal tract; and, there being no ciliary folds (except a few dorsal and ventral ones in a few species, as also in the rays among the elasmobranchs) there is really no discrete ciliary body at all. The uvea is much alike from ora terminalis to pupil (Fig. 67, p. 159), and unless one calls this whole region 'iris' one must

define the latter rather arbitrarily as 'the portion of the anterior uvea which is visible through the cornea', in order to distinguish the remainder as a ciliary body.

The ciliary muscle fibers run from the inner surface of the rim of the cornea to the outer surface of the chorioid at or near the ora terminalis, and because of this disposition were long called a 'tensor chorioideæ' muscle, and were believed to tauten the chorioid around the vitreous to maintain turgidity and an unvarying optical situation during the movements of the lens. The chorioid is too firmly plastered onto the sclera anteriorly to make the need of such an action plausible, however, and at present we are helpless to explain the teleostean ciliary muscle as anything but a phylogenetically precocious, 'orimentary' or pre-adaptive structure, of unknown but minor importance, which very conveniently hung on until the reptiles found an important job for it.

By and large, teleosts are more or less myopic—up to as much as 15 diopters, the highly abnormal telescope gold-fish even more so. This is to be expected, since approaching the lens to the retina would only put their eyes out of focus for any and all distances if they were not myopic to start with. Their eyes are thus set for close work with a minimum of effort, and they need to exert muscular force only when attending to distant objects—and 'distant', for the average fish in the average natural body of water, means only up to fifty feet at most. Beyond this distance underwater vision—anything more than light-sense—is practically nil. Many mud-grubbing, small-eyed fishes are hypermetropic, indicating a loss of importance of vision to them, for which we will see an exact analogy among the mammals (*v. i.*).

Other Fishes—Of these we can say little. Nothing is known concerning accommodation in the living cladistians, *Polypterus* and *Calamoichthys*. Nothing whatever is known as yet concerning the eye of the newest 'living fossil', the crossopterygian *Latimeria chalumnae*.

Dipnoans appear to have no accommodation. In the small-eyed forms, at least, there is no ciliary body, no zonule, no lens-muscle. In *Lepidosiren* and *Protopterus* this is comprehensible, for the whole eye, and particularly the retina, is so very crudely built as to make accommodation a useless refinement. The relatively large eye of *Neoceratodus* deserves further study. This lungfish does not æstivate in mud, and spends much of its time at the surface of the water (see Fig. 61a, p. 137), where its eyes should be quite useful.

The 'ganoids', too, need more attention. Hess was unable to detect any accommodatory changes in the sturgeon. The eyes of the spoonbills (*Polyodon* and *Psephurus*) have not been studied from any standpoint, to say nothing of accommodation. In the holosteans (*Amia, Lepisosteus*), there is an ectodermal lens-muscle, but it is not known whether it is homologous with that of the elasmobranchs or with that of the teleosts; nor is it even certain whether it pulls the lens forward, or backward and sidewise.

Matthiessen's Ratio—The optics of the fish eye—of whatever taxonomic category—was exhaustively studied years ago by Matthiessen. This worker found that the fish eye is more thoroughly standardized than any other. The refractive index of the lens nearly always varies parabolically from 1.51 at the center to 1.38 (as in mammals) at the surface, giving it a higher effective index (1.649–1.653) than that of any other vertebrate type. The lens is a sphere, and the optical properties of the other media are constant, the indices of the humors low (about equal to water—1.33+), so that the difference between lens- and humor-indices is maximal. Thus the fish eye should always have the same proportions regardless of its size—and indeed Matthiessen found close agreement to exist between the theoretical and the actual. The distance from lens center to retina, for instance, should ideally be 2.55 times the radius of the lens, and it rarely actually differs from this figure, known as Matthiessen's ratio, by more than one or two integers in the last decimal place—even in the tubular eyes of deep-sea forms, which were once called telescopic because they were thought to be radically different from ordinary fish eyes in their optical principles.

Optical Elimination of the Cornea—The conformation of the fish cornea is of no consequence whatever, since its refractive index is so near to that of water that it has no focusing power. It is not surprising to find that the piscine corneal epithelium is often irregular in thickness, the cornea sometimes having concentric ridges and the like which would be fatal to clear vision in a land animal. All responsibility for image-formation rests on the lens, which, for the sake of periscopy, must lie against the cornea and even project from the level of the head surface if this is feasible. This necessity has kept the fishes using their ancient methods of accommodation; for until, in land animals, the cornea came to share in refraction, thus allowing the lens to be drawn back farther into the eye,

there was no way in which pressure could be conveniently brought to bear upon the equator of the lens to change the radii of curvature of its surfaces.

Consequences of Lens Movement—The very fact that the fish lens is never required to change its shape affords one advantage, however, for the lens is enabled to be firm and thus to have a relatively high index of refraction—reaching, in one silurid, a value of 1.72+, which is rather higher than that of most optical glass. The axis of the fish eyeball can consequently be its shortest diameter, thus economizing a bit upon space in the head. But the shiftings of the lens during accommodation introduce a complication whose existence is often neglected: the aqueous humor being incompressible, the lens can move only if the aqueous is free to get out of its way. In the lampreys, the deformation of the globe in accommodation results in no actual change in volume of the anterior chamber, for the lens remains always in contact with the cornea. In the teleosts, when the lens is drawn backward by the retractor lentis, the aqueous in the posterior chamber is free to flow through the pupil, if need be, to keep internal pressures balanced. But in the elasmobranchs the forward movement of the accommodating lens tends to seal off the anterior chamber by pressing the lens against the pupil margin, for there is no canal of Schlemm. These fishes have consequently had to leave unclosed a small portion of the embryonic fissure, at the root of the iris, so that the aqueous can flow readily between the anterior and posterior chambers.

Amphibians—The amphibians are not completely emancipated from the water, and a few frogs and salamanders never leave that medium for a moment; but the eyes of amphibious amphibians have undergone wholesale modification, for vision through air, both as regards the structure of the globe and the production of protective adnexa. The cornea comes into its own here as the principal refracting structure, the lens becoming merely adjuvant to the accommodatory adjustment of the location of the image. The anterior chamber is deepened by the regular dome-shape taken on by the cornea, so that the eyeball is practically spherical (Fig. 106); and the lens lies much deeper in the eye than in fishes, since it no longer needs to protrude through the pupil. Closer responsiveness of the iris to the intensity of illumination is thus permitted, and the photomechanical changes of the retina here begin their phylogenetic degeneration (see Table II, p. 150).

The entrance of the cornea into the optical picture, together with the elongation of the axis of the eyeball, has permitted the lens to flatten somewhat in land forms. The ratio of its equatorial and axial diameters is around 1.3 : 1 instead of 1 : 1 as in fishes and aquatic salamanders. The lens does not owe this slight flattening to tension in the zonule as in our-

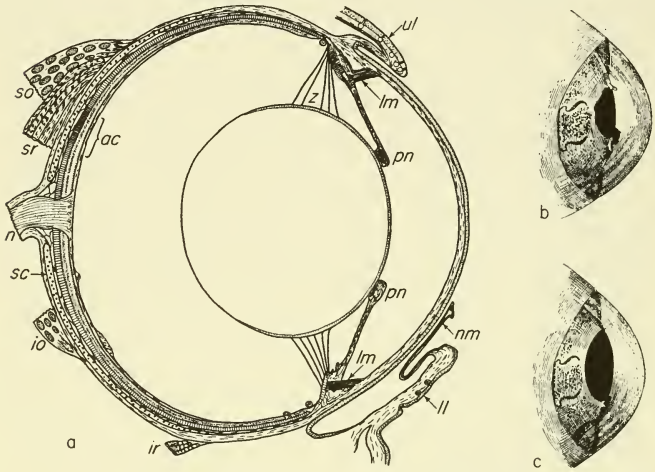

Fig. 106—The amphibian eye and its accommodation.

a, anuran eye in vertical section. × 11½. Based largely on *Rana pipiens*.

ac- area centralis (marked by local concentration of visual cells); *io*- inferior oblique; *ir*- inferior rectus; *ll*- lower lid; *lm, lm*- lens muscles (protractors); *n*- optic nerve; *nm*- nictitating membrane (transparent, independently movable portion of lower lid—not homologous with sauropsidan and mammalian nictitans); *pn, pn*- pupillary nodules (urodeles have only the ventral one, and only the ventral lens muscle); *sc*- scleral cartilage; *so*- superior oblique; *sr*- superior rectus; *ul*- upper lid; *z*- zonule (fibers are embedded in vitreous).

b, anterior segment of *Bufo* sp., in relaxation. × 3. From Franz, after Beer.

c, same as b; in accommodation; note forward movement of lens.

selves, however; for, despite the fact that the amphibian lens is in such a position that it might be changed in shape, it is rather firm and is changed only in position, for accommodatory purposes, just as in all fishes.

The amphibian mechanism of accommodation is a close imitation of that of the elasmobranchs; but the muscles involved are mesodermal

ones, rather than ectodermal. The amphibian zonule is more distinctly fibrous than that in lower forms, but is not so well extricated from the vitreous. Vitreous substance fills that space between the radial zonule fibers which, in a mammalian eye, would be an aqueous-filled 'canal of Hannover' with its contents communicating freely with those of the posterior chamber (see p. 19). There is scarcely any ciliary body—it is just wide enough to form an attachment for the peripherally converged fibers of the zonule. The more-or-less radial 'ciliary folds' of frogs are really *iris* folds on the back face of that organ. Mid-ventrally however there is one heavy fold which deserves to be called a ciliary process, and it is to this that the ventral (in salamanders, the only) protractor lentis muscle inserts, running from its origin at the sclerocorneal junction through the root of the iris. The protractors are thus not connected directly to the lens, but their pull is communicated to it by the ciliary 'processes' and the bundles of zonule fibers attached thereto.

The delicate zonule fibers fan out to the equatorial zone of the lens from the neighborhood of the annular hyaloid vessel which lies on the minute ciliary body. Since the site of origin of the fibers is so narrow, the lens can move forward and backward without much hindrance from them.

Unlike the elasmobranchs which also pull the lens forward, the anurans have a canal of Schlemm, though a discontinuous one consisting of a dorsal and a ventral crescent. Accommodation is too rapid, however, to afford time for aqueous to escape from in front of the advancing lens by diffusing into the canal, and there is no convenient open slit through the iris root mid-ventrally, for this slit (see p. 265) has been occupied by the ventral protractor lentis muscle. Hence the urodeles (which lack the canal) have produced a nodule of hard connective tissue at the mid-ventral point of the pupil margin, which lifts the iris free of the lens capsule locally, and allows the aqueous to flow around to the back of the lens as the latter moves forward. Anurans ordinarily have a dorsal pupillary nodule as well (Fig. 106a, *pn*), corresponding to a second, dorsal, protractor lentis muscle. The ciliary muscle is no better developed in amphibians than in teleosts, and is no more obviously useful in any way.

Newts are emmetropic under water; and in the air, where the cornea comes into optical play, they would become very strongly myopic. Frogs are emmetropic in air. Under water, they of course become strongly hypermetropic, and are quite unable to compensate therefor with their limited range of forward lens-movement. No amphibian has as much as five diopters of accommodation, and many apparently have none at all

—particularly the most secretive forms with the most active pupils, whose crude eyes mediate mere light-sense rather than form-sense (*e. g., Megalobatrachus japonicus*). The refraction of toads has not been much studied; but land forms might be expected to be emmetropic or myopic in the air, and hypermetropic when in the water during the breeding season. Toad rods are longer than frog rods, helping to reduce the need for accommodation, though toads (Fig. 106b, c) do have more accommodation than frogs anyway. *Salamandra* is known to be emmetropic in air.

Rôle of the Vitreous in Ichthyopsidan Accommodation—The vitreous humor is an important part of the mechanism of accommodation in the Ichthyopsida, although this is not at first apparent. The original vertebrate eye did not at first possess any semblance of a zonule, and without the jellification of the mass of fluid lying behind the lens, the latter could not be held in place (*cf.* Fig. 103, p. 258). In the vertebrate-like eye of a squid (Fig. 1g, p. 3), where the tough 'epithelial body' serves as a zonule, the 'vitreous cavity' behind this lens-holding plate of tissue is filled with watery liquid, not with a jelly. In the lampreys, the elastic cushion of the vitreous keeps the lens propped against the cornea and insures that the position of the resting lens will always be the same at every relaxation of accommodation.

In the elasmobranchs the gelatinous, discoid zonule, though far less strong than the tissue 'zonule' of a cephalopod, might perhaps restore the lens to position after relaxation of the protractor lentis, even if the vitreous were not jelled. In the teleosts, however, the elasticity of the vitreous is needed to serve as a quick-acting antagonist of the retractor lentis, which must work against it and could not single-handedly replace the lens simply by elongating in relaxation.

According to this idea, the vitreous—or at least its gel condition—is ordinarily a useless vestige in the higher vertebrates and has only persisted because (being transparent) it does not interfere, and affects nothing but the distribution of accommodatory deformation between the anterior and posterior lens surfaces. It returns to usefulness however in the snakes, and in those few amphibious reptiles, birds, and mammals which squeeze the front of the lens with the sphincter iridis, tending to force the lens backward. This tendency must be controlled by the cushioning action of the vitreous, and by the zonule fibers acting as check ligaments; else in these animals, the efforts of the iris to increase the refracting power of the lens would be nullified by a decrease in the distance from lens to retina.

Sauropsidan Muscles of Accommodation—With the advent of the Sauropsida the eye underwent a considerable revolution, especially as regards the mechanism of accommodation. None of the great changes involved is even hinted at in any extant amphibians, and their production therefore cannot be traced. In the reptiles, pro- and retractor lentis muscles are finally abandoned, though a new mesodermal lens-moving muscle, the transversalis, makes its appearance in turtles and lizards and is concerned with swinging the lens sidewise in the eye, toward the nose, thus aiding in the convergence of the two visual axes for the purposes of binocular vision (Fig. 111, p. 278).

The sauropsidan method of accommodation involves an actual peripheral squeezing of the lens, the power coming from a ciliary muscle which, compared with the puny one in the Ichthyopsida, is massive indeed. The whole ciliary body is conspicuous and elaborate. Its muscle fibers, and those of the iris as well, differ greatly from those of fishes and amphibians in that they are of the striated type, histologically, instead of smooth. How profound a difference this may make physiologically, we do not really know. Striated muscle elsewhere in the body differs from smooth muscle in being ordinarily voluntary, in having no inherent rhythm of contraction, in greater rapidity of action, and in its propensity for easy fatigue. But the smooth muscles of vertebrate eyes are not quite like those of the rest of the body. The dilatator iridis is not a fully-differentiated muscle at all, though it and the sphincter iridis are physiologically and pharmacologically indistinguishable (despite their ectodermal origin) from somatic smooth muscles or from the ciliary muscle, which has more in common with somatic muscles embryologically. Human accommodation is notoriously fatigable, this being the usual basis of 'eyestrain'; but whether the residence of the fatigue is the muscle itself, we do not know.

We hardly know what to expect from the striated sauropsidan homologues of these contractile structures. Would they, like the striated muscle of the heart, contract rhythmically if denervated? This has not been tested. Are they voluntary? The iridic muscles of birds certainly seem to be—but so do the smooth-muscled irides of a few mammals. Are they unusually fatigable as compared with the corresponding mammalian muscles? Of this, we know nothing.

If any one of the usual differences between smooth and striated muscles does exist here, to serve as a 'reason' for the change, it would seem to be the greater rapidity of contraction of striated muscle. If striated

intra-ocular muscles were known only in the birds, we would be ready to argue that they had been developed for rapidity of action, without waiting for experimental proof—for common sense would tell us that the fast-flying birds must need extra-rapid accommodation. The situation in the birds' only vertebrate competitors, the swift fruit-bats, seems corroborative; for it is easy to say that the reason why the Macrochiroptera have given up all efforts to accommodate, and have produced the substitutive retinal deformation described above, is because the early mammals inherited only slow-acting, smooth intra-ocular muscles from their particular reptilian ancestors (see Fig. 60, p. 135)—or else had returned their ciliary muscles to an unstriated condition before the bats evolved.

But what need have the plodding reptiles for any ultra-rapid accom-

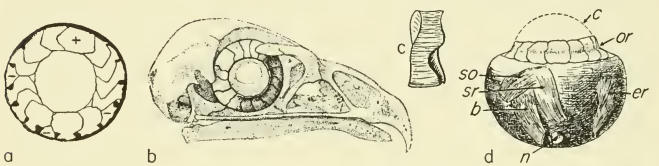

Fig. 107—Scleral ossicles in sauropsidans. After Edinger.

a, ossicular ring of *Sphenodon punctatus*, with '+' and '–' ossicles designated. × 1½. b, skull of an eagle, *Aquila chrysaëtos*, with ossicular ring in place. × ⅜. c, single ossicle of *A. chrysaëtos*. × 1. d, eyeball of albatross, *Diomedea regia*, showing how ossicles support the concavity of the corneoscleral junction. × ⅔. *b*- bursalis muscle; *c*- cornea; *er*- external rectus; *n*- optic nerve; *or*- ossicular ring; *so*- superior oblique; *sr*- superior rectus.

modatory capacity? Many lizards, of course, are remarkably agile—and of all land reptiles the lizards have the most extensive and rapid accommodation. But this is most marked in the chameleon, than which no vertebrate (unless it be the sloth) moves more slowly—except for its lightning-like tongue. The answer is that these and other lizards are insectivorous: they need rapid accommodation as much because of the speed of their prey as because of their own rapidity of movement. And even a turtle has been seen to strike and grasp a grasshopper in flight.

Scleral Ossicles in Sauropsida—The sauropsidan sclera typically consists largely of a cartilaginous cup whose open rim extends quite close to the limbus of the cornea. Just as typically the remaining zone of the sclera is occupied by a circlet of thin overlapping plates of bone, the scleral ossicles (Fig. 107). These are lacking only in crocodilians and

snakes—the latter also lacking the scleral cartilage, among a great many other ocular structures which other sauropsidans possess. The scleral ossicles are not convexly curved to continue the rotundity of the equatorial sclera smoothly into the sharper curvature of the cornea. On the contrary they are flat or even concave, so that the whole zone of the sclerocorneal junction is depressed or concave to form a broad annular sulcus (Fig. 107d). This sulcus is important to the fundamental processes of sauropsidan accommodation. The ossicles which are responsible for it are therefore considered here as a part of the mechanism of accommodation in these vertebrates.

There is little question as to the evolutionary source of these ossicles, but the time of their origin is in doubt. Surrounding the eyes of fishes is a ring of small skull bones, the circumorbitals. The overlying skin often bears a sense organ (of the lateral line system) centered over each of the

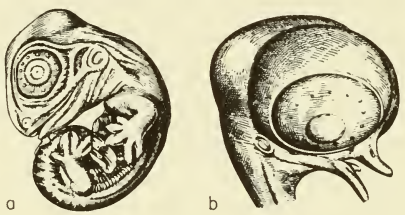

Fig. 108—Sauropsidan embryos, showing sensilloid papillæ at periphery of cornea: evidence for the origin of scleral ossicles from extra-ocular bones (see text). From Franz, after Dabelow.

a, *Lacerta agilis*. b, *Vanellus* sp.

circumorbital bones. In sauropsidan embryos the scleral ossicles arise as dermal bones which sink into the sclera, and the ectoderm over each one temporarily shows a sensilloid papilla (Fig. 108). It thus appears that the scleral ossicles are homologous with the originally *extra*-ocular circum-orbital bones.

Another theory derives the sauropsidan scleral ossicles from the scleral bones of fishes, which being co-existent with the circumorbital bones could scarcely be homologous with the latter. Ancient armored fishes had four plates in the anterior sclera, forming a closed ring. Modern fishes show at most only two of these—if they are indeed homologues. In some swift swimmers, the tuna and swordfish for example, the two plates are joined to make a complete ring and are protective against the impact and distortive pressure of the water (see Fig. 130, p. 380).

These oligomeric ossicular rings of fishes have been dubiously homologized with the polymeric ones of the Sauropsida through two question-

TABLE VIII—

			LENS MOVED FORWARD BY:	LENS MOVED BACKWARD BY:	LENS POWER INCREASED BY:	
FISHES	Lampreys		elasticity of eyeball	extra-ocular (cornealis) muscle		
	Elasmobranchs		ventral, ectodermal protractor muscle	relaxation		
	Holosteans		?	?		
	Teleosts		relaxation	ventral, ectodermal retractor muscle (rapid-acting in littoral spp., such as blennies)		
	All others					
AMPHIBIANS	Anurans		dorsal & ventral, mesodermal, protractors	relaxation		
	Urodeles		ventral, mesodermal protractor muscle	relaxation		
	Cœcilians					
REPTILES	*Sphenodon*				these muscles are striated: ciliary (Brücke's) muscle	
	Crocodilians					
	Turtles					
	Lizards				ciliary (Crampton's, Brücke's) muscles	
	Snakes		mesodermal muscle in iris root presses iris against vitreous, & indents sclera; vitreous, under pressure, pushes lens forward	relaxation	pupil sphincter, in amphibious spp.	
BIRDS	Terrestrial spp.				Brücke's & Crampton's muscles; may also be a Müller's *	
	Amphibious spp.				Brücke's (Crampton's lacking); circular fibers in *Morus*	
MAMMALS	Most					
	Aquatic	Sea-cows				
		Whales			toothed: Brücke's, may be Müller's; baleen: little or no ciliary muscle	
	Amphibious	e.g. otters			Brücke's (& Müller's?) muscle(s)	
		Seals				
	Primates	Man			elasticity of lens capsule, released by muscle = *real* force: Brücke's and Müller's muscles	
		Others				

*Not the same 'Müller's muscle' as that of mammals; see text.

MECHANISMS OF ACCOMMODATION

	ACCESSORIES & SUBSTITUTES		REFRACTION*	EXTENT OF ACCOMMODATION	REMARKS
	oculomotor muscles antagonize corneal?		−8D (*Lampetra fluviatilis*)	>8D	
	stenopaic pupils in rays & *Scylliorhinus*		+10-15D	15-20D	slit at iris root allows transfer of aqueous
			?	?	lens-muscle present, function not known
	small ciliary muscle, function not known		as much as −15D (in water) in good-eyed spp. (*Anabas*, OD in air)	probably ordinarily enough to overcome the myopia (*Anabas*, no accomm.)	stenopaic pupil in *Enchelio phis*
					prob. no acc. (unless in *Neoceratodus*)
			strictly aquatic spp. OD in water; amphibious & terrestrial spp. probably all OD in air	never >5D (never enough to abolish the hypermetropia of a land sp. under water)	pupillary nodules allow aqueous transfer
					probably have no accommodation
sclera ossicles and annular pad of lens allow ciliary body to bear directly on lens			?	?	nocturnal, but ossicles retained (has a fovea!)
			OD, or nearly so, in air; strongly + in water	probably never >2D	nocturnal—ossicles have been discarded
	sphincter of iris aids considerably		marine spp. OD in water, all others OD in air	more than enough to give emmetropia in H_2O	less acc. in marine & strictly terrestrial spp.
	stenopaic pupils in most geckoes		OD	great	Crampton's muscle may 'sharpen' cornea
	pupil becomes stenopaic in sea-snakes, when out of water		+2-9D	0-17D	muscle of accomm. in iris derived from Brücke's muscle
	muscle cells in chorioid perhaps 'focus' foveæ		OD (*Apteryx* is myopic)	great	Crampton's muscle increases focusing power of cornea
	sphincter of iris usually aids; often 'lens' in nictitans		OD (penguins are — in air)	very great (cormorants: 40-50D)	kingfishers: a unique accommodation-obviating device (text!)
	stenopaic pupils, ramp retinae, in some (see text); fruit-bat retina		as much as +1D (very small eyes, high +)	usually little or none, but may be up to 4D	Brücke's muscle may be present, but with no apparent function
			(*Dugong*) −5D in air, ∴ strongly + in water	apparently none	no ciliary muscle
			unknown	toothed: presumably considerable; baleen: not more than 1/2-1D	
	very powerful iris sphincter aids greatly		OD	more than enough to give emmetropia in H_2O	
	in air, pupil is a slit, & cancels astigmatism		high myopia & corneal astigmatism in air, nullified by slit pupil	enough to restore emmetropia in water	astigmatism eliminated when under H_2O
			true normal +1/2D (?)	about 10D at age 21	highly variable (like domesticated spp.)
	stenopaic pupil in *Tarsius*		OD, or as high as +1D (baboons are myopic)	not >10D	

*D=diopters; +=hypermetropia; −=myopia; 0 (zero)=emmetropia

able links: an imaginative reconstruction of one extinct crossopterygian fish which postulates a polymeric ring, and the situation in the extinct amphibians (the Stegocephali).

Irregular bits of bone occur in the sclera of *Triturus pyrrhogaster,* and the Brazilian frog *Stereocyclops* (=*Hypopachus*) *incrassatus* has an ossified annulus around the cornea; but in no modern amphibian can any certain counterparts of the sauropsidan ring be found. The stegocephalians, however, had 'scleral ossicles'. These usually numbered 20-32 and were set in several rows. Moreover, they almost always formed only a dorsal half-moon—rarely a closed and single ring. These bones may have been homologues of the piscine circumorbitals, but it is much more likely that they formed a sort of mail on the upper lid and were thus a part of the head armor which was characteristic of the group and indeed gave it its very name. And even if they were indeed in the sclera, they could not have been involved in accommodation, for they formed only part of a circle.

The whole mechanism of accommodation which we are here calling 'sauropsidan'—including the scleral ossicles—may really have been invented by the stegocephalians, which were certainly diurnal and may have had sufficiently acute vision to make an excellent accommodation worth while. But if so, the right stegocephalian for showing the origin of the ossicular ring has not yet been found fossil. It may be significant that of the cotylosaurs, the stem-group of the reptiles, no specimen has yet turned up showing scleral ossicles.

The scleral bones number sixteen or seventeen in *Sphenodon.* They were lacking in *Pleurosaurus,* the largest aquatic rhynchocephalian relative of *Sphenodon,* thus affording an interesting comparison with the modern crocodilians in which the ossicles probably disappeared upon the advent of nocturnality, with its crude images and consequent uselessness of accommodation. The Mesozoic marine crocodiles had them—at least in the sidewise-looking Metriorhynchidæ and in *Pelagosaurus,* the one member of the Telosauridæ whose eyes were not directed upward.

Modern reptiles and birds have fourteen plates more often than other numbers. Fourteen are usual for lizards, though there may be as many as sixteen or as few (*Chamaleo*) as eleven. Turtles have still lower numbers—König found from six to nine in *Testudo græca,* ten in *Emys orbicularis.* Birds have up to eighteen, the passerines having fourteen. Phylogenetic schemes based upon ossicular numbers have been attempted, but unsuccessfully.

The bones may be so dovetailed into each other that the ring is immobile (Fig. 107b, c), or they may so overlap that they can slide on one another; but there is no experimental evidence that they ever do so. 'Plus' and 'minus' plates are distinguished as to whether they overlap both of their neighbors or are overlapped by both, and these exceptional plates tend to occur in the vertical or the horizontal meridians, or both (Fig. 107a). There is always an unusual situation mid-ventrally (where either a '+' or '–' plate or an edge-to-edge junction without overlap occurs)—attributed to the disturbance of the formation of the plates created by the embryonic fissure of the optic cup.

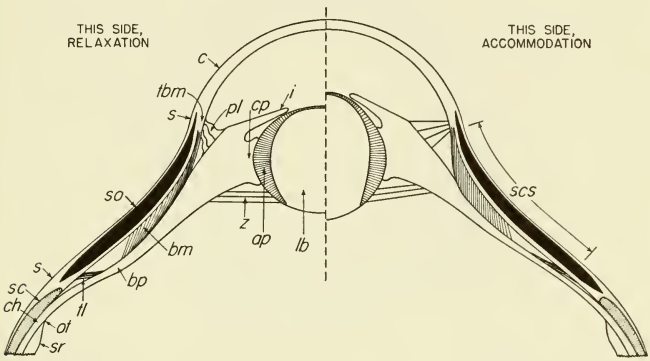

Fig. 109—Diagram of generalized reptilian mechanism of accommodation.

ap- annular pad of lens; *bm-* Brücke's muscle; *bp-* base plate of ciliary body; *c-* cornea; *ch-* chorioid; *cp-* ciliary process; *i-* iris; *lb-* lens body; *ot-* ora terminalis; *pl-* pectinate ligament; *s, s-* sclera; *sc-* scleral cartilage; *scs-* sclerocorneal sulcus; *so-* scleral ossicle; *sr-* sensory retina; *tbm-* tendon of Brücke's muscle (continuous with inner layers of corneal substantia propria); *tl-* tenacular ligament; *z-* zonule.

Accommodation in Sauropsida (Except Snakes)—The production of a sulcus is the whole meaning, physiologically, of the sauropsidan ossicular ring. It stiffens the concavity against the force of the intraocular pressure which, if unresisted, would evaginate it. This pressure rises slightly during accommodation, which it does not do in fishes, amphibians, or mammals. On examining a sagittal section of a sauropsidan eye we see the internal result of the sclero-corneal sulcus: an approximation of the ciliary body to the lens.

This is further aided by two other devices, the ciliary processes and the 'Ringwulst', or 'annular pad' (Fig. 109). Ciliary processes are to be sharply distinguished from ciliary *folds*. The latter may be radial or circular and are always low affairs whose significance is solely the increase of the secretory or absorptive surface of the thin layer of blind retinal tissue which covers them, the ciliary epithelium. The folds on the posterior surface of the amphibian iris (there being no room for them on the narrow ciliary body) are in the same category.

Ciliary processes differ morphologically from ciliary folds only in a quantitative way, but they have a separate physiological significance. They are tall, fin-like structures (Fig. 110) and serve to bring the ciliary body into firm contact with the lens, with which (in Sauropsida) their tips are actually fused. The ciliary body, if it lacked them, might still be made to reach to the lens equator and contact the annular pad smoothly all the way around. But, there would be two difficulties about such an arrangement. The more grave one would be that the retrolental space would be sealed off from the posterior chamber so that aqueous could not transfer back and forth between the two during accommodation, as it is free to do between ciliary processes. Also, the ciliary body would tend to be 'muscle-bound', with a great deal more internal friction during the action of its muscles, if its constrictive force were not transferred indirectly to the lens through the ciliary processes. If one imagines the spaces between the processes to be filled in with solid material, one can see that as the ciliary zone decreased in diameter, this material would have to be compressed; and the energy required for this useless compression would be lost from the effective action of the ciliary muscle upon the lens. Only the lizards have been able somehow to reduce the size of the processes almost to the vanishing point and still employ the standard sauropsidan method of accommodation. They may have some difference in the mechanics or hydraulics of the phenomenon which accounts for their heresy.

While the scleral ossicles and the ciliary processes extend the ciliary body axiad to meet the lens, the latter comes half-way, so to say, by its production of the annular pad. In Sauropsida, after the ordinary circumferential lens fibers have been laid down, the lens epithelium in the equatorial region does not remain simply cuboidal or columnar. Its cells elongate enormously, without swinging their axes through 90° to become ordinary circumferential lens fibers (compare Fig. 109, *ap*, with Fig. 41a, p. 111). The result is an equatorial thickening on the lens,

whose elements are radially disposed and thus admirably oriented for their service as architectural columns, transmitting the radial stress of the ciliary processes directly to the spherical heart of the lens. The annular pad has no optical function whatever, for the iris shields it and the image-forming light beam is confined to the more onion-like nuclear portion of the lens. Like the softness of the lens in Sauropsida, the thickness of the annular pad, as might be expected, goes with activity

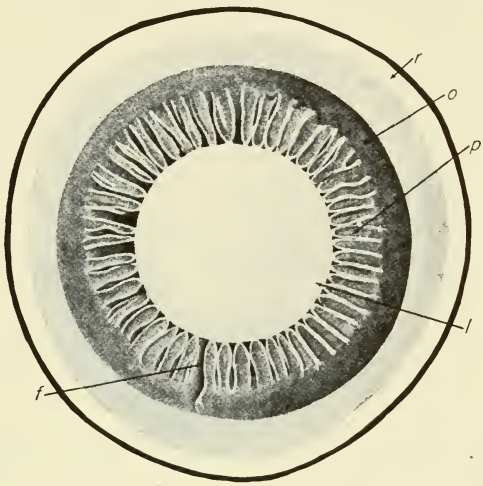

Fig. 110—Anterior segment of left eye of a turtle (*Emys orbicularis*), seen from behind, showing junction of ciliary processes with lens capsule (characteristic of sauropsidans—contrast Fig. 44, p. 115). × 13. After König.

f- unclosed portion of embryonic fissure; *l*- lens; *o*- orbiculus ciliaris; *p*- ciliary processes; *r*- sensory retina.

of the ciliary muscles, in its variation from species to species. It is thickest of all in the chameleons.

The ciliary muscles in birds and lizards have the same location as those of non-lacertilian reptiles, but are more complicated, as is explained below. The fibers of sauropsidan ciliary muscles are all meridional except in a very few species, and have their origin in the inner layers of the cornea at its margin. Their insertions are not into the chorioid, as in the Ichthyopsida, but are scattered along the orbiculus ciliaris much as in the

mammals. There is often a tenacular ligament (*tl* in Figs. 109, 112) running from the sclera to the orbiculus just in front of the ora terminalis, which prevents the chorioid's being drawn forward. Thus when the ciliary muscle contracts, it can have but two possible actions—and only the first of these unless the sclerocorneal sulcus happens to be quite well marked: (*a*) a stretching of the orbiculus and a heaving of the corona of ciliary processes forward and toward the axis of the eye, thus pressing them against the lens. Any actual forward movement of the lens is checked partly by the weak suspensory-ligament fibers, partly by the 'pectinate ligament' running from cornea to iris root across the angle of the anterior chamber (Fig. 109, *pl*). The force of contraction of the ciliary muscle is thus largely diverted to the accomplishment of an actual squeezing of the lens. (*b*) A traction backward and axiad upon

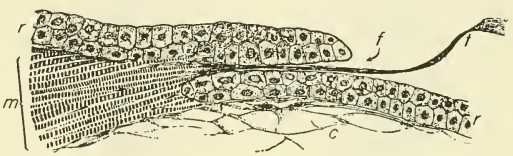

Fig. 111—Transversalis muscle of a lizard, *Lacerta serpa,* as seen in a frontal section through the region (mid-ventral) of the embryonic fissure. After Läsker.

c- connective tissue of ciliary body; *f*- unclosed portion of embryonic fissure; *m*- transversalis muscle; *r, r*- pars ciliaris retinæ; *t*- tendon of muscle, which inserts on lens.

the limbus corneæ, deepening the sclero-corneal sulcus and sharpening the curvature of the cornea.

How much of the latter action (*b*) ever occurs in reptiles is a question. It would be helpful in accommodating the eye for near objects; but most of the accommodation is certainly brought about by the sharpening of the anterior curvature of the lens. The posterior surface of the lens abuts upon the relatively unyielding vitreous, and the periphery of the anterior surface against the similarly firm iris root. Hence most of the deformation of the lens is confined to a central area on the anterior surface—just as it is, by an utterly different mechanism, in the human eye (see Fig. 109, p. 275; *cf.* pp. 32-4 and Fig. 14, p. 31).

It used to be thought that a deformation of the sclero-corneal region, impressing the vitreous and causing the latter to push the lens forward, was the chief or only factor in sauropsidan accommodation. Ingenious experiments made a few years ago by Hess, however, have shown that the

general processes described above are what actually take place. Hess proved that there is no increased pressure on the vitreous, by showing that in an excised eye the process will occur quite normally under electrical stimulation, even though the posterior half of the eyeball be cut away.

Even though the lens does not move forward very far, it *bulges* forward and encroaches upon the anterior chamber. The birds (except the nocturnal ones) have left patent that same meridional, ventral slit in the anterior uvea which we remarked in the elasmobranchs, to permit the equalization of anterior and posterior chamber pressures. Despite this provision, the aqueous pressure rises a little as noted above. In lizards and turtles, the transversalis muscle runs through an homologous aperture (Fig. 111; see Fig. 110, *f*).

The details of the accommodatory process in the crocodilians (which have no scleral ossicles) remain to be worked out. The group has had less attention than others, perhaps because material is hard to obtain in Europe. Our abundant alligator is going begging for want of a curious American physiologist. All that is known is that it does accommodate, though very slightly and slowly. The beast is emmetropic, or a diopter or so hypermetropic, in air. Under water, it must be 15-20 diopters or more hypermetropic.

Special Features in Birds and Lizards—The accommodating equipment of birds differs from that of reptiles only in minor respects. The transversalis muscle (never, apparently, concerned with accommodation so much as with binocular vision) has been found only in the pigeon. It may not be an homologue of the reptilian one, but rather an aberrant slip of the ciliary muscle itself.

The birds share with the lizards one muscle, Crampton's, which is unique but is clearly a derivative of the ordinary reptilian ciliary muscle. The reptilian ciliary, which is a husky descendant of the little ichthyopsidan tensor chorioideæ, runs from the corneal margin and the inner surface of the anterior sclera to the base-plate of the orbiculus ciliaris. The situation in the birds is as if this reptilian ciliary muscle had been cut in two all the way around the eye, half-way back along its course, the two halves then being stretched enough to let the cut ends overlap (Fig. 112). Crampton's muscle represents the corneal end of the reptile ciliary. Near its posterior, inner surface is seen the insertion of a second (Brücke's) muscle which continues backward toward the ora terminalis. Brücke's

muscle thus represents the posterior portion of the ancestral reptilian ciliary. Brücke's name is often applied to the whole of the ciliary in forms below the birds, as well as to the radial or meridional portion of the mammalian ciliary muscle where this has given rise (as in primates) to a

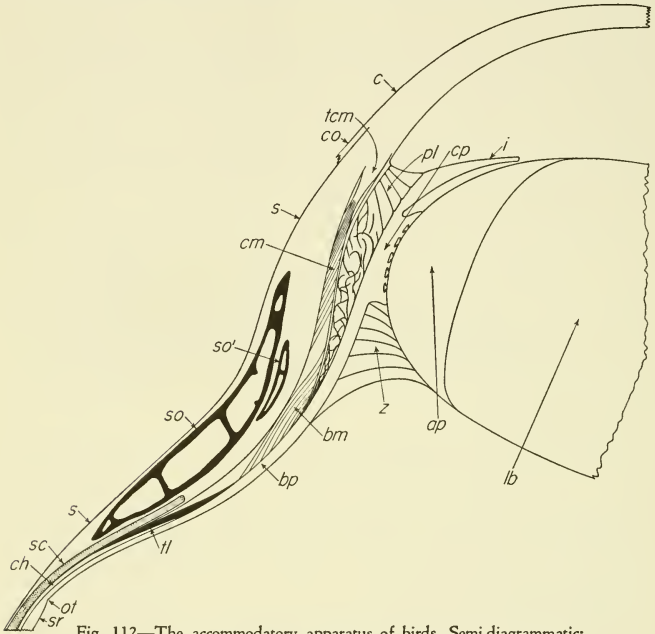

Fig. 112—The accommodatory apparatus of birds. Semi-diagrammatic; based upon the situation in the hawks.

ap- annular pad of lens; *bm-* Brücke's muscle; *bp-* base plate of ciliary body; *c-* cornea; *ch-* chorioid; *cm-* Crampton's muscle (entirely intrascleral); *co-* conjunctiva; *cp-* ciliary process; *i-* iris; *lb-* lens body; *ot-* ora terminalis; *pl-* pectinate ligament; *s, s-* sclera; *sc-* scleral cartilage; *so-* scleral ossicle; *so'-* overlapped portion of adjacent scleral ossicle; *sr-* sensory retina; *tcm-* tendon of Crampton's muscle (continuous with inner layers of corneal substantia propria); *tl-* tenacular ligament; *z-* zonule.

circular 'muscle of Müller'. Quite another 'Müller's muscle' occurs in some birds, where it is simply the posterior portion of a further-subdivided Crampton's muscle, with its fibers still radial in orientation. In lizards, Crampton's muscle is even more distinct from Brücke's than it is

in birds, for it is completely embedded in the sclera. Brücke's muscle inserts, not upon Crampton's, but upon a partition of scleral material.

The anatomical and physiological divorce of the anterior part of the ciliary muscle from the posterior, together with the especially deep sclerocorneal sulcus of birds, seems designed to promote the cornea-deforming action which we noted was possibly present, though not marked, in reptiles. At least, it is in the birds which have the heaviest Crampton's muscles (hawks and owls) that the cornea changes most in shape during accommodation. Again, in diving birds, whose corneæ are extra-thick and stiff, and of no optical use under water anyway, Crampton's muscle is all but absent.

Another, and little-understood, muscular apparatus of bird eyes which may have something to do with accommodation is found in the fundal portion of the chorioid. Here (particularly, it is claimed, in the neighborhood of the fovea) there are scattered short, thick muscle cells running rivet-fashion through the thickness of the chorioid. It has been suggested that these, by varying the thickness of the chorioid, serve to adjust very precisely the position of the fovea in accommodation. Their action would be comparable to that of the fine adjustment of a microscope, the ciliary muscles being the coarse adjustment. It is as likely that they regulate the blood volume of the chorioid and thus affect vitreous-cavity volume and pressure during accommodatory changes or changes in altitude during flight. In some birds these chorioidal muscle elements are striated, in others smooth, in still others absent; and until these differences have been studied further and correlated with other avian features, intra-ocular or extra-ocular, we will have no certainty as to quite what they mean. If they are indeed a micrometer adjustment for accommodation, they may explain why avian foveal cones are not elongated, as are those of other foveate animals in which such elongation relieves the accommodation of the necessity of being extremely precise (see p. 182).

Most birds are emmetropic or a little hypermetropic, but the wingless kiwi (*Apteryx*) is somewhat myopic. This nocturnal bird is reputed to have poor vision at all distances, especially in the daytime; and it unquestionably has the poorest eye, all-round, of any bird. As would be expected, diurnal birds have somewhat more extensive accommodation than any reptiles, the extent of accommodation being related to their feeding habits (see p. 366). Even such ordinary-eyed birds as the domestic hen and pigeon have a range of eight to twelve diopters; but the owls have half of this or less. The homer, whose vision is probably better than

that of any other breed of pigeon, has been found experimentally to have a near-point at 40 centimeters. This implies that there is a considerable hypermetropia in the resting eye.

Snakes—Turning to the snakes, we find that all sauropsidan rules are off. As is explained fully in Chapter 16, the snakes seem to have originated as animals whose way of life was such as to allow the eye to degenerate extensively. Among the parts lost from the equipment handed on to them by their good-eyed lacertilian ancestors were such items as scleral cartilage, scleral ossicles, ciliary processes, annular pad, and (the eye being very badly off indeed for a time!) iris muscles. In modern snakes, the sclera is fibrous as in higher mammals, the eyeball consequently spherical.

The snakes eventually had to make good all of these losses as best they could. The ciliary body being far out of contact with the lens, and with its proper musculature stolen by the iris to become a revamped pupillomotor apparatus, it is quite out of the picture of accommodation. The only intra-ocular muscles are the mesodermal ones of the iris, which have been taken into the iris secondarily from the ciliary body. These muscles, along with their new job of operating the pupillary aperture, have had to retain the function of accommodation which they had when they were in the ciliary body, but perform that function in an entirely new way:

The iris is pressed forward into a strongly conical shape by the spherical lens (Fig. 154, p. 456). At its root there is a powerful aggregation of sphinctral fibers—those which have moved least from their old position in the ciliary body. When these fibers contract, they draw in the sclerocorneal junction and put a pressure upon the vitreous which it in turn communicates to the back of the lens. The main body of the sphincter, near the pupil, and the more-or-less radially disposed iris fibers also contract simultaneously. The conical iris tries to flatten back into a plane, augmenting the backward pressure upon the vitreous. The end result is that the firm lens moves bodily forward, without appreciable change in shape, a third to a half of the distance from its resting position to the cornea. The cornea may also move forward a little, due to an elongation of the eyeball which compensates for a reduction in its equatorial diameter by the pull of the iris. Accommodation in the snake eye is thus accomplished essentially as in the eye of the squid (in which, likewise, the intra-ocular pressure is raised in accommodation), and resembles that of only the elasmobranchs and amphibians among the vertebrates; and even there only to the extent that the lens is fixed in

shape (water snakes excepted) and moves forward, adjusting the eye for nearer objects. The physiological indentation of the anterior scleral region is so pronounced that the sclera may even have a couple of permanent meridional furrows anteriorly, in readiness for their further deepening during accommodation.

Beer found that in a snake eye in which the posterior sclera had been cut away, and in which the accommodatory action was evoked electrically, the lens moved *backward*. This was due to the (unbalanced) rise of anterior-chamber pressure, which in the intact eye is far exceeded by the rise in vitreous pressure, so that the lens has to move forward. According to Beer, various snakes are anywhere up to nine diopters hypermetropic, but most have more than enough accommodation to overcome their refractive error.

In some snakes, particularly those with a fovea (*Dryophis* and *Thelotornis*), there is a nasad component of the forward motion of the lens. This is exactly equivalent, in its optical consequences, to the nasad movement of the lens of a teleost when the accommodation is relaxed to adjust for near objects. The same basis obtains in the two cases: a strongly temporal position of the area centralis in the retina (see Fig. 79, p. 186; *cf.* Fig. 77, p. 185, and Fig. 105d, p. 261).

Mammals—As with peoples and their governments, vertebrate eyes get the kind of accommodation they deserve. The degree of 'eye-mindedness' in the subphylum sinks from the higher fishes to the amphibians, rises sharply in the reptiles, still higher to a peak in the birds and falls off woefully again in the mammals—with some recovery in the highest forms and a very considerable one in the squirrels and simians, to be sure. The engineering efficiency of the accommodatory apparatus runs exactly parallel with this variation in the value set upon vision.

The mammals originated as small-bodied, small-eyed, forms which were almost certainly nocturnal. Within the marsupial and placental series, parallel evolution has culminated in the production of swift, large-bodied, large-eyed types (the kangaroos on the one hand, the ungulates on the other), adapted to open country, where good vision is more valuable than to a forest animal. Such animals have expanded their visual capacities to twenty-four-hour performance and some have gone on close to diurnality, with a steady increase in visual acuity. The more eye-minded forms, with much sharper vision than their primitive relatives, may also have much more extensive accommodation. But since their evolution passed through the bottle-neck of the monotremes, opossums,

and insectivores (see Fig. 60, p. 135), they have had to get along with whatever portions of the beautiful sauropsidan mechanism those antique nocturnal mammals happened to retain.

That was not much, for aside from the ciliary muscle itself—and this has retrograded to the unstriated type—not one of the sauropsidan adjuncts to vigorous accommodation remains in any mammal. Though a slight circumcorneal sulcus (marked in apes and man) may be present, it is not an indentation of the sclera itself and is never supported by scleral ossicles; nor is there ever an annular pad on the lens. The monotremes have a vestige of the pad and have kept the scleral cartilage, thus presenting a tunica fibrosa which is matched in the sauropsida only in the crocodiles—likewise nocturnal and primitive within their class. In no mammal are the ciliary processes joined to the lens capsule, and in only a few are they ever even in light contact with it during accommodation. This simplification of the mammalian eye, giving it an essentially amphibioid make-up, has led one prominent phyleticist (Franz) to suggest that the placental mammals were derived from forms intermediate between the amphibians and the reptiles, with only the monotremes and marsupials (the former having scleral cartilage, and both groups showing double cones and oil-droplets in their retinæ) tracing back to fully differentiated reptiles.

The comparative anatomy and palæontology of the occipital condyles would seem to make such a diphyletic origin of the mammals quite impossible. The placental mammals lack so many of the sauropsidan ocular structures, not because their ancestors never had them, but because the small-eyed sub-insectivores were so strictly nocturnal that they discarded these daytime features as so much excess baggage. The oldest known mammals averaged less than rat-sized and are indicated, by their dentition, to have been insectivorous and granivorous. Wherever among the placental mammals very small size has reappeared, even the inferior mammalian mechanism has failed to evolve, or has been allowed to disappear.

The most important result of the wholesale discardments of reptilian ocular structures in the mammals has been to take the ciliary body out of intimate contact with the lens—especially far out, in the simians and the echidnas, despite the breadth of their lenses. Those semi-diurnal and diurnal mammals which have rebuilt an effective accommodation have consequently (like the snakes) been under the necessity of developing a brand-new method.

This method, seen at its best in man (see Chapter 2, section B), makes use of the elasticity of the lens capsule to furnish the actual force of accommodation. The contraction of the ciliary muscle, by easing the tension in the fibers of the zonule which normally hold the lens flattened, merely releases this elastic force and lets it go to work. In some amphibious mammals, as in the turtles, water-snakes, and diving birds, the sphincter iridis comes into play also to aid in accommodation (Chapter 11, section C). Even in these mammals, the ciliary muscle still apparently does most of the work, for it is more massive than in strictly terrestrial species.

Their employment of capsule elasticity is probably wholly original with the mammals. The elasticity is not a useful factor in sauropsidan accommodation which can be regarded as having been simply exaggerated by the mammals. Reptilian lenses do take on something like their accommodated shape, when they are cut free from their attachments. But the zonule fibers are probably not under greater tension in the resting eye than in the accommodating one, as they are in mammals. More likely their tension increases in accommodation, since they apparently serve as check-ligaments rather than as the real supports of the lens.

Among the land mammals, the ciliary muscle is well developed only in ungulates, carnivores, and primates. It is seldom so compact as in man. More often there is much connective tissue between the fibers, so that although the muscle is bulky, it is not strong. In many small, large-lensed mammals (*e.g.*, mice) it consists of but a few fibers, or is even entirely lacking. Even where it can be made out easily, as in domestic ungulates, it may accomplish nothing because of the great size of the lens and the relative weakness of the capsule. The horse, sheep, and pig have no accommodation, and such instances serve to emphasize that though the ciliary muscle may propose, it is the elasticity of the lens capsule which disposes—just as in a presbyopic human being.

Circular ciliary muscle fibers, forming a 'muscle of Müller' with an especially efficient orientation (see p. 33), are known to occur only in seals, primates (best in man) and in some toothed whales and some ungulates. This distribution is important to remember; for every so often someone comes along with experiments based upon pharmacological responses, which 'prove' that the radial and circular portions of the ciliary muscle in mammals are *antagonists,* the circular fibers adjusting the eye for near and the radial ones, just as actively, for distance. Such

work, it will be found, is always done upon cats or perhaps rabbits—neither of which has any circular fibers whatever.

The whole ciliary body may be so oriented as to put the ciliary muscle at an advantage or at a decided disadvantage, because of great interspecific variations in the shape of the mammalian eyeball which in turn are due to considerations which happen to be more important to the eyes concerned than accommodation. Thus in the prosimians the ciliary body may be tubular like the eye itself (Fig. 84b, p. 213), while in sirenians and whales it may lie in a plane continuing that of the iris (Fig. 140b, p. 409; Fig. 141a, p. 413).

Like the vitreous humor, the ciliary processes in the terrestrial mammals and man are functionless vestiges so far as mechanical importance is concerned. Any such importance disappeared as soon as the processes lost their former approximation to the lens, for the accomplishment of which the reptiles evolved the processes themselves, the scleral ossicles, and the annular pad. They do serve as convenient attachments for some of the zonule fibers, but would seem not to be indispensable in this connection. They have persisted presumably because, as with ciliary folds and iris folds, their great contribution to the aqueous-secretory surface is valuable for the regulation of the intra-ocular pressure. Franz sharply distinguishes between two types of processes in different species: a rugose, vascular kind (*e.g.*, man—see Fig. 6c, p. 14) and a thin, relatively avascular kind (*e.g.*, cat). The meaning of these differences is not surely known, but they imply a difference in secretory capacity.

According to Lindsay Johnson, wild mammals normally show a slight hypermetropia (up to one diopter), which is better for animals which do no close work with hands than myopia would be. Myopia is normal only for mandrills and other baboons, which is comprehensible considering that these are the only sub-human primates which have abandoned the trees for a life on open ground, where food objects are smaller. A little hypermetropia is even better than emmetropia for most mammals of any size, for two reasons: *(a)* because with increasing age the lens hardens and its index of refraction rises, making an emmetropic eye become somewhat myopic as time goes on. An initial hypermetropia will delay this change to a greater age of the animal, by allowing 'slack' for the rise in refractive power before that rise results in a myopia; and *(b)* because since a hypermetropic eye must accommodate a little even at long object-distances, the tonus of the accommodatory muscles is always fully developed and the apparatus is alert for the performance of any needed

change of setting. If an eye is one diopter hypermetropic, it needs only one diopter of accommodation in order to make itself emmetropic, and thus obtain sharp images all the way to the horizon. And with only *two* diopters of accommodation, it can give itself a near-point at one meter—ordinarily quite close enough, for any animal that cannot read!

Among zoo animals and domesticated ones, just as with auto-domesticated—*i.e.*, 'civilized'—man, anything may happen. In fact, it is wholly unsafe to draw ecological conclusions from any situation in domestic species. Less than fifty per cent of horses are emmetropic; and though myopia is most unusual for a wild mammal, it is extremely common in zoo animals and barnyard varieties.

Along with their normal slight hypermetropia, ungulates usually show a slight horizontal astigmatism, probably a consequence of their efforts to widen the visual field horizontally by every possible means (see pp. 299-300). The extent of accommodation is very low indeed in mammals—often zero—except in the primates. The cat, which is the nearest competitor of the simians in this regard, has but half the accommodation of a thirty-year-old man and loses even this in old age. Human accommodation being 'tops' for mammals (Beer found no more than ten diopters in any ape), it is desirable to turn back to the graph (Fig. 15, p. 35) showing its extent at various ages. The senescent diminution of the power of accommodation in mammals is bound up with the accommodatory method itself. Certainly in the Ichthyopsida no such falling-off is to be expected, for the lens in these animals may become even harder with age than it is in the young, without this affecting the range of accommodation a particle. In the Sauropsida, the direct action of the ciliary muscle probably accomplishes an effective alteration of lens form at ages where, if the animal were a mammal of the same relative age, the lesser force of the elasticity of the lens capsule could no longer make headway against the sclerosis of the lens fibers.

A special situation arises in small-eyed mammals. The squirrels are exceptional among the rodents, in having some accommodation, which we should expect from their diurnality and high visual acuity. The European squirrel may be emmetropic or as much as one-half diopter hypermetropic, and can accommodate from one to one and one-half diopters. As the size of the eye diminishes from that of a cat to that of a mouse (Fig. 71, p. 173), the increasing (relative) size and firmness of the lens and its (relative) recession toward the retina results not only in the reduction of accommodation from a couple of diopters to nothing, but

also in an increase of the hypermetropia from a half-diopter or so to five, seven, even ten diopters. This situation has been branded as a disharmony, supposedly inevitable in small eyes simply because they are small. This notion ignores the optical perfection of even smaller fish eyes. The apparent disharmony simply reflects the indifference of mice and mouse-sized mammals in general to any refinements of vision relating to resolving power. The cerebral images of mice and the like are so crude at best, that the eye is useful more for recording the intensity and direction of light, and the motion of large objects in the visual field, than for discrimination of pattern. In such animals, the 'nose knows' far more about the environment than does the eye.

(B) Visual Angles and Fields

In all vertebrates, vision predominates in any accurate localization of objects in space. Aside from vision, only audition and olfaction are telæsthetic senses—that is, capable of giving information about objects and events at a distance. The distance and direction of an object which is beyond arm's reach can be only crudely judged by these other telæsthetic modalities, and can be accurately evaluated only through vision if at all. Audition is notoriously untrustworthy as a means of localization. The finding of an object by olfaction is a trial-and-error process, and is not localization at all in the sense of a pre-knowledge of location.

The visual registration of space entails the embracement, by the retinæ, of light rays coming from many directions. The animal may be thought of as having its head at the center of a sphere of space. The proportion of that sphere within which the animal can see is influenced by several factors:

A. The visual angle, in various meridians, of each eye;

B. The position of the eyes in the head and the ratio of binocular field to total visual field;

C. The orientation of the visual axes, where these do not coincide with the anatomical optic axes;

D. The capacity for reflex and voluntary eye movements and the location of the area centralis or fovea, if one is present;

E. The capacity for head movements in compensation for any severe reduction of visual angle or eye mobility.

Visual Angles—The angle—or rather, cone—of space subtended by the retina is surprisingly uniform throughout the vertebrates. It is rarely much greater or much less than 170°. This angle is influenced by the angular extent of the retina. If the functional retina comes far forward in the eyeball, as in the horse, the eye may see through an angle much greater than 180°. If the tissue is restricted to the fundus of a tubular eye like that of the owl, the visual angle may be as little as 110°, and is still smaller in deep-sea fishes.

The visual angle is affected also by the cornea, though not in a way which is self-evident. If the projected area of the cornea in the plane of the limbus be divided into the area of the retina, a quotient is obtained which one might suppose to represent the visual angle. This quotient has been found to be 13.5 for man, 11.5 for a falcon, 10.4 in the pigeon, 4.0 in an owl, only 2.5 in a bat. The visual angles of these eyes do not bear such numerical relationships to each other. The cornea-retina quotient expresses rather the concentration of light upon the retina and affects the sensitivity of the eye, not its visual angle. If, however, we consider the angular size of a cornea—the portion it includes on a sphere of its own curvature—we have a better indication of the angle of space which that cornea will place upon the retina behind it—provided the retina's own angular size is great enough to receive all of it, which is not always true as for instance in the owls. The human cornea subtends only 60° of a circle with its own radius, and is relatively small. That of the cat occupies 107°. A single human eye sees through 150°, a cat eye through 200°. The bending of the light rays as they pass through the cornea accounts for the apparent discrepancy of the visual angle (which is the effective angular extent of the retina) and the angular size of the cornea. Where the angular size of the retina exceeds that called for by the properties of the cornea, obviously the anteriormost part of the retina must be non-functional. This is true, for example, of the human retina in a zone which extends backward for three millimeters from the ora terminalis. This zone is blind, and is said to contain no rhodopsin.

A very special case is that of the chameleon, whose thick circular lid, fused to the cornea, leaves a crater-like opening the size of the immobile pupil, through which the eye has only 'tube vision' with the whole periphery of the retina unable to receive light. One might wonder why the chameleons have not pared away this useless peripheral portion of their eyes as the owls have done. Perhaps it is because they have needed to retain the hemispherical shape of the back of the eyeball to enable it to

roll smoothly in the orbit during their extensive eye-movements. Ordinarily, the eyelids impose no restriction upon the visual angle of the eye. We can look up and see our eyebrows, which means that they are concealing a part of space from us; but we cannot see our lid margins, even as unfocused shadows.

Another special case is that of the fish. The cornea having the same refractive index as the water, it is optically eliminated. The lens then takes over the control of the visual angle; but, being spherical, it imposes no limitation at all and the visual angle is thus determined in the last analysis by the angular extent of the retina. The strongly refractive fish lens usually protrudes from the level of the surface of the head, and is oftentimes able to place much more than 180° of space upon much less than 180° of retina (Fig. 128, p. 376)—at least in the horizontal plane, where an aphakic space often helps out considerably.

Position of the Eyes in the Head—Many a careless writer has stated that phylogenetically, 'from fish to man', there has been a gradual migration of the eyes from a position back-to-back to one in which the two lines of sight are forward and parallel. Actually, a complete series of eye positions can be arranged wholly within the fish group, another such series within the birds, and a third within the mammals. Scattered species elsewhere have the lines of sight parallel, but directed upward rather than forward. The development of a frontal position of the eye from an initial lateral one has taken place several times independently. Some cases of 'frontality', as for example in deep-sea fishes (see Fig. 138, p. 403) have rather special interpretations. But by and large one finds a good correlation with predacity: the hunters tend toward frontality so as to have the best vision of the prey they are pursuing, while the hunted tend to retain laterality of eye position so as to be able to detect an enemy coming from any direction. The predaceous animal can afford not to have such 'eyes in the back of his head', because his offensive weapons, teeth and claws, give him immunity from stealthy attack. Carnivores rarely make a habit of feeding upon other carnivores, for the risks are too great and the meat is too tough.

The most important effect of variations in the positions of the eyes is to vary the extent of the binocular field and the direction in which it lies—usually forward, but sometimes more or less upward. The binocular visual field is simply the spatial cone or zone within which the separate monocular fields overlap. Its value to the animal and the character of

vision within it will be discussed in detail farther on. Suffice it to say at this point that two eyes are better than one, and that vertebrates in general have seemingly striven to enlarge their binocular fields at the expense of their uniocular ones (uniocular being used here to denote the part of a monocular field which is not overlapped by that of the other eye). Animals which have clung to strong laterality have done so in obedience to powerful factors, such as defenselessness (*e.g.*, rabbits) or total absence of cover in the environment (*e.g.*, pelagic fishes), which make the retention of periscopy vitally important. The various degrees of partial frontality are compromises between the urge for binocularity and the need for periscopy.

In most groups of vertebrates the predaceous habit is a very common specialization; so, the associated tendency toward frontality is likewise common. Remembering that the visual field of a single eye is roughly constant at 170° or so, we may consider the angular width of the binocular field to be quite directly related to the angle between the two optic axes, which in itself will depend upon the position of the eyes in the head.

Extent of the Binocular Field—There are very few vertebrates indeed which are known for certain to have no binocular field whatever. The lampreys, the hammerhead sharks and a few large-headed teleosts, such chunky amphibians as *Cryptobranchus,* the penguins of the genus *Spheniscus,* and the larger whales constitute these exceptions. In some other animals, as the chameleons and probably some fishes, there is no binocularity when the eyes are at rest but it can be created by convergent eye movements. Wherever the eyes are mobile, there exists the theoretical possibility of widening the binocular field by convergence of the optic axes; but as we shall see, this possibility has been realized only in forms which have developed an area centralis with or without a fovea, for only such forms have any ability to move the eyes at will.

The extents of the static binocular and uniocular fields have been estimated for many animals by different means at various times. Over a century ago, the positions of the eyes of a great number of vertebrates were judged by Johannes Müller from the angle between the planes of the two orbital rims. Müller assumed the optic axes to be perpendicular to these planes. In 1877, Grossman and Mayerhausen also published a long list of figures, based upon the divergence of the axes of the two corneæ. In modern times these patient researches have had to be discarded, for the optic axis is neither normal to the plane of the orbit

margin nor necessarily coincident with, or even close to, the visual axis —the actual physiological line of sight in fixation (*cf.* Figs. 3, 16; pp. 7, 37).

Paradoxically, the optic axis can be considered to be the visual axis only when there really is no visual axis—that is, where there is no area of acute vision or fovea and hence no fixation or precise aiming of the eye at objects. In mammals there is usually an area, but it is central (except in ungulates) and here the orientation of the optic axis does become a fair criterion of the direction and extent of the binocular visual field. Lindsay Johnson's chart of mammalian inter-axial angles (Fig. 113, p. 297) is therefore acceptable; but a similar chart for fishes (whose foveæ are strongly temporal) would be worthless as indicating the direction of best vision with the eyes at rest.

The best studies have been the recent ones of Rochon-Duvigneaud, Kahmann, and Piša, who have made direct determinations of the visual fields by observing the trans-scleral images of a movable light, in dissected heads clamped in a perimeter. Most of our accurate knowledge of visual fields in animals has come from these investigations.

In fishes, Kahmann found that the binocular field measured usually from 20° to 30° in the horizontal plane. There were wider variations among the marine forms, where the angle might be as small as 4° (*Box, Trigla*) or greater than 30° (*Trachurus, Cepola, Serranus,* certain labrids, and especially in flatfishes). Among freshwater forms the widest binocular fields, and thus the greatest degree of frontality, were in such predators as the trout, perch, and pike, with values ranging from 30° to 40° or more. But on the marine side the predaceous *Julis* revealed a value of only 15° and the mackerel-like *Lichia,* 8°. A great surprise to Kahmann was the low value of 14° for the archer-fish, *Toxotes jaculator* —which, by analogy with the snakes which have the habit of striking and hence have similar visual requirements, might be expected to have as wide a field as *Dryophis* (*v.i.*). One fish, *Chlorophthalmus agassizii,* probably does rival *Dryophis,* for it is reported to have a strikingly similar pupil (see Fig. 79, p. 186). In one type of chondrostean, the spoonbill or paddlefish *Polyodon spathula,* the eyes are aimed forward about as frankly as in some deep-sea fishes (see Fig. 138b, p. 403). But since they are set on the dorsal side of the 'paddle' near its base, their view downward is cut off.

Because of their periscopy, nearly all fishes also have something of a dorsal binocular field. Bottom-dwelling fishes have truly specialized such

a field, and it amounts to 25° in some star-gazers (genus *Uranoscopus*), 30°-40° in some of the blennies, and to still higher values in other star-gazers (*Astroscopus**), in many batoids and flatfishes, and in such forward-and-upward-lookers as the toadfish, *Opsanus tau*. Purely accidental and of little value on the other hand, is the narrow posterior binocular field which many fishes possess. The nasal retina is too crude for them to make any real use of such a field. A ventral or downward binocular field is useful to pelagic fishes, and some surface forms (needlefishes, halfbeaks, flyingfishes, the look-down [*Vomer setipinnis*] etc.) have their eyes canted downward to produce one; but in most fishes the angle between the optic axes in the vertical plane is concave upward.

Amphibians nearly all have a binocular field, wider in anurans than in urodeles and much reduced or absent in some of the latter; but no exact determinations appear to be on record. The horizontally oval pupil of most frogs and toads would tend to extend the binocular field a bit, but its primary meaning is probably in connection with periscopy.

The reptiles show less variation than the fishes (see Table IX, next page). The crocodilians have about 25° of binocular field. In the turtles, one extreme is given by the herbivorous *Testudo* (18°), and the other by the snapping turtle, *Chelydra* (38°). Two-thirds of the snapper's food is animal, and half of this consists of game fishes. The snapping turtle strikes its prey like a snake, and thus has special need of the good distance-judgment which binocularity confers. The lizards have the strongest laterality of the eyes, with binocular fields of only 10° to 20° as a rule. Though most species are predaceous their prey is small; but the lizards themselves have much to fear from predaceous birds and mammals, and have therefore retained their periscopy. The monitors (Varanidæ) are big enough to fear nothing, however, and anticipate their supposed descendants, the snakes, with values of 30° or more. In snakes the binocular angle ranges mostly between 30° and 40°, with higher values in strongly eye-minded, striking snakes such as *Dryophis*, whose key-hole pupil is a clever device for widening the binocular field without this being (as it is in *Zamenis flagelliformis*) at the expense of periscopy. The river-snakes, *Acrochordus javanicus* and *Cerberus rhynchops*, have an extensive binocular field which is directed largely upward, but these forms seem not to be guided by vision at all. Kahmann states that they 'tongue'

*The species of *Astroscopus* stare fixedly upward. In this genus the eye-muscles are much reduced, and portions of one or more of them have been converted into a huge electric organ, occupying the enlarged orbit in which the small eye has been crowded forward.

Table IX

VISUAL FIELDS IN REPTILES (After Kahmann, rearranged)

Groups and species	Angle between optic axes, degrees	Width of monocular field, degrees	Width of binocular field, degrees
Turtles			
Chelodina longicollis	110	.....	.....
Testudo ibera	.....	.....	18
Geomyda trijuga	.....	.....	30
Clemmys caspica	.....	.....	34
Chelydra serpentina	.....	.....	38
Crocodilians			
Alligator mississippiensis	.....	152	24
Caiman niger	144	.....	.....
Caiman sclerops	.....	160	26
Lizards			
Trachysaurus rugosus	.....	158	14
Anguis fragilis	.....	158	16
Tiliqua nigrolutea	.....	160	18
Lacerta viridis	172	156	18
Iguana tuberculata	169	158	18
Physignathus lesueuri	.....	154	20
Ophisaurus apus	.....	144	20
Chalcides ocellatus	.....	.....	20
Basiliscus plumifrons	172	154	22
Zonurus giganteus	.....	160	22
Varanus griseus	146	.....	32
Snakes			
Trimeresurus wagleri	141	.....	.....
Chrysopelea ornata	136	.....	.....
Leptophis liocercus	131	.....	.....
Python molurus	137	.....	.....
Coluber longissimus	.....	158	20
Coluber leopardinus	165	.....	20
Tarbophis fallax	.....	146	24
Zamenis dahli	.....	.....	28
Diemenia textilis	.....	158	30
Zamenis gemonensis	.....	158	32
Vipera berus	.....	150	32
Constrictor constrictor	.....	160	34
Natrix viperinus	136	168	34
Malpolon monspessulanis	160	160	38
Thamnophis sirtalis	.....	160	40
Uromacer oxyrhynchus	.....	.....	40
Denisonia superba	110	152	40
Bitis gabonica	.....	.....	40
Natrix natrix	.....	156	42
Zaocys carinatus	.....	.....	42
Dispholidus typus	.....	164	42
Zamenis flagelliformis	.....	.....	46
Dryophis prasinus	.....	166	46

abundantly under water; and in *Cerberus* he was unable to detect any power of accommodation.

Among the birds we may distinguish straight-headed forms like the pigeon and the song-birds, whose eyes are laterally aimed (Fig. 70, p. 172), from round-headed predaceous species such as swallows, goat-suckers, hawks, and owls, with more or less frontality—the optic axes never diverging more than 90° (Fig. 115, p. 309). Some penguins (*Spheniscus* spp.) have no binocular field, and consequently weave and sway a good deal when they are scrutinizing an object. Others, like the Adélie penguin, look binocularly at far objects and when walking, also at near objects when they are angry; but they turn the head sidewise and look monocularly in any calm examination of a near object. Whether the shoe-bills, toucans, and such birds have had to sacrifice all binocularity for the sake of their huge bills, is not known.

The parrots have the smallest binocular fields of any so far measured in birds—6° to 10° in most species. An exception, of course, is the flightless, nocturnal owl parrot or kakapo of New Zealand (*Strigops habroptilus*) which has strong frontality and a considerable (but unmeasured) binocular field. Another New Zealand bird is quite unique: the rare blue or mountain duck, *Hymenolaimus malacorhynchus*. Whereas all other ducks fixate monocularly, this species has the eyes aimed forward, and fixates binocularly like a hawk.

Granivorous birds never have over 25° of binocularity, and many have less than 10°. The homing pigeon, for instance, has been found to have a 24° binocular field upon full convergence, with a total field of 340°-342°. In line with the generalization stated above concerning predacity, the insectivorous birds and herons have higher values and in the hawk group the binocular field varies from 35° to 50° or more. Owls have 60°-70°; and considering their marked frontality the hawks and owls would have even wider binocular angles were it not for the fact that their monocular fields are so restricted by tubularity. The round-headed ostriches and their allies also have wide binocular fields but no exact figures are on record.

The most exceptional birds are the snipes, as exemplified by the woodcock. Every hunter knows that in the bizarre 'timber doodle' the eyes are set far back on the head—so far that the posterior binocular field is probably much wider than the anterior. The bird's feeding habits afford an explanation: the long bill is thrust so deeply into the ground after worms and the like, that the bird would be most vulnerable to attack when feed-

ing, were its eyes not positioned as they are. Another interesting peculiarity is seen in the various genera of bitterns. When alarmed, these birds freeze, with the bill canted up into the air at a steep angle, making themselves as tall and slender as possible so as to blend with the rushes among which they stand. Any binocular field in an anatomically anteriad direction—that is, along the direction of the bill—would then be aimed uselessly at the sky; but the bitterns' eyes can be turned so far ventrally that they can see binocularly around and under their own chins, and thus truly forward and parallel to the ground (Fig. 116, p. 309).

The mammals are mostly large enough so that the eyes are carried well above the ground. Few of them therefore have the optic axes tilted at all upward as they are in most other terrestrial vertebrates. The exceptions are the platypus, some rodents (particularly the beaver), insectivores, bats, a few 'edentates', and the seals. In the platypus, the beaver, and the seals, the upward tilt is strong and constitutes a definite adaptation to keep the eyes in the air while swimming awash. In the whales there is a marked downward tilt, for these forms have abandoned all hope of seeing into the air. The sea turtle *Chelonia mydas* also shows this ventrad slant of the optic axes, which diverge downward at 150° from each other, in line with the habit of floating at the surface and keeping watch below for possible food. A similar situation in synentognath fishes has already been mentioned (p. 293).

The angles between the optic axes of various mammalian groups and species are shown in Figure 113, which brings out graphically the differences, in this respect, between the pursuers and the pursued. Among the most defenseless of all mammals are the rabbits, whose optic axes are nearly in a straight line. The anterior binocular field in different kinds of rabbits has been found to vary from 10° to 34°. Lindsay Johnson estimates that a hare has monocular fields of 190°, overlapping both anteriorly and posteriorly*. The European squirrel, too, is claimed to see behind him with the eyes at rest. Toward the other extreme there range the carnivores, with the lords of brute creation, the cats, rivalling man in their degree of frontality—the axes diverging only from 4° to 9° in different species. The higher primates seem anomalous in their possession of completely parallel optic axes, for they are not predatory. A

*Indeed, Arthur Thompson states that the brown hare (*Lepus europæus*) makes a habit of *not* looking directly ahead when running. The animal is credited with keen sight—it is claimed to watch the eyes of an enemy, and to flee if looked at directly; but it may run almost into a man, particularly if the latter is standing in a furrow down which the hare is speeding.

totally unrelated and unique habit, that of manipulation, accounts for the development of frontality by the primates as we shall see later.

The total visual field of mammals varies with the attitude of the optic axes, from 360° in some rodents through 250° in the dog, to 180° in a man whose eyes are in the position of rest. The situation in the horse has been studied with particular care. Here, the temporal boundary of the visual field runs backward parallel to the axis of the body, so that the posterior blind area is not angular and constantly widening with increasing distance. Thus the horse—when he holds his head up—cannot be approached unawares from behind by any object bigger than his own head. Anteriorly, the limits of the two monocular fields each cross the

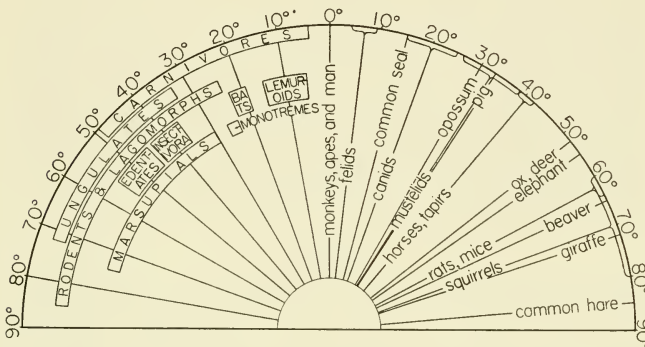

Fig. 113—The angle between the optic axis and the body axis in various mammals. Redrawn, modified, from Lindsay Johnson. Families and sample species are shown on the right side of the chart, larger taxonomic categories on the left.

body axis and make 35.5° angles therewith, thus giving the horse a 71° binocular field together with nearly complete periscopy. Each eye sees through an angle of 215°, which is probably a record unless it is exceeded in some of the fishes. Some of the special devices which make possible this wide monocular visual angle in the horse will be mentioned shortly. According to Kahmann, mammals in general possess binocular fields ranging in width from 20° (or less) to 40° in the rodents, to 120° or more in the cats and prosimians and a maximum of 140° in the simians and man. The ungulates are intermediate with values from 60° to 80°,

as are also the majority of frontolateral-eyed carnivores such as the mustelids and viverrids. Among the carnivores, the domestic cat is preëminent with (according to Thieulin) a binocular field of 130° and a total visual field of 287°—thanks to the large, prominent, and strongly curved cornea.

Of course, the binocular field of any animal is more narrow above and below than it is straight ahead, and it is ordinarily pear-shaped. Again, the cone of binocular space does not necessarily begin immediately at the eyes—there is often a blind region, in front of the snout (Fig. 128, p. 376), which may extend forward for a fraction of an inch, or for a foot or more as in *Varanus* and in large fishes. In chicks, it has been claimed that it is just this distance (a couple of inches) from which the bird regards each kernel before pecking at it.

Piša has studied the domesticated mammals and has mapped the form of their binocular fields. These tend to be tall, narrow pear-shaped areas unlike the roundish one of man. In man, the uniocular fields are reduced to a pair of crescents which are but 30° wide in the horizontal meridian and taper to points above and below the binocular field. Some of Piša's values for the divergence of the optic axes and the maximal width of the binocular field are given in the accompanying table:

TABLE X

VISUAL FIELDS IN DOMESTIC MAMMALS (After Piša, rearranged)

Animal		Divergence of optic axes, post-mortem	Greatest width of binocular field
Horse		127°	57°
(Foal)		118°10′	62°40′
Cow		113°5′	51°40′
Goat		103°	63°25′
Dogs	Setter	44°10′	78°40′
	Greyhound	33°20′	82°40′
	Fox Terrier	52°50′	90°20′
	Rattler	40°20′	116°20′
Guinea-pig		103°25′	76°30′
Rabbit		141°24′	.....
	At rest	.....	27°
	Aroused	.....	32°
	Posterior binocular field	.....	9°

Devices for Enlarging the Binocular Field—Aside from eye movements (which we shall shortly consider) there have been evolved various devices, both static and dynamic, for enlarging the binocular field despite the handicap of ocular laterality imposed by the presence of an indispensable snout or beak. These devices are of very diverse nature, but are best described here under the only heading that unifies them.

Two of them occur in fishes—the aphakic space, and the temporad movement of the lens in accommodation. The aphakic (*i. e.,* lensless) space is widespread in teleosts, and often consists of an anterior extension of the basic circle of the pupil into an egg-shape, with the narrow end of the egg pointing forward. One can see into the eye through the narrow end of the egg, past the lens whose center is opposite the big end of the egg (Fig. 105f, p. 261). It was long debated what the fish saw *outward* through the aphakic space; but we now know that he looks through it only with the temporal part of the retina, and thus through the lens after all. Were it not for the aphakic space, the line of sight could not be so nearly parallel to the body axis. Again, when the lens is drawn backward by the retractor lentis muscle, there is a considerable temporad component of the motion (Fig. 105). In those fishes which have a fovea, the fovea is always temporal in location (Fig. 77b, p. 185), and the lens in accommodation moves temporally more than it moves backward toward the fundus. This shifts the effective visual axis more nearly parallel to the axis of the body.

The ungulates are conspicuous for their broad, horizontally oblong pupils (Fig. 85c, p. 218), which extend the visual field somewhat (see Fig. 90b, p. 225) in the horizontal meridian (*v. re* the horse, above) and hence help to enlarge the binocular field. The frogs, the marmots, and two carnivores (*Cynictis* and the Meerkat, *Suricata*) employ the same trick, though not nearly so effectively. The snakes *Dryophis* and *Dryophiops,* and the probably unrelated *Thelotornis,* not only have the keyhole pupil with its aphakic portion lined up with the center of the lens and the temporal fovea, but also have excavated a groove on the side of the head in front of the eyes, along which the eye looks ahead (Fig. 79, p. 186). In *Dryophis* at least, the lens during accommodation moves not only forward but also more strongly nasally than in other snakes—a device which accomplishes, in reverse, the same end as that attained by the foveate fishes. The transversalis muscle of turtles and lizards (see p. 279) likewise moves the accommodating lens nasally as well as slightly ventrally. This is probably of especial help to the lizards, for their eyes

are placed so far laterally, and have so little mobility, that they are in need of all possible means of converging their visual axes intra-ocularly.

The most conspicuous and common of all of these arrangements is the static condition which may be termed 'nasad asymmetry', characteristic of some marine (but not freshwater) fishes, many lizards, all birds, ungulates and carnivores (*e.g.* cougar, Fig. 71, p. 173). It expresses itself in a permanent anatomical tilting of the cornea and lens toward the snout, so that a line through their centers (the true visual axis) strikes the retina far temporally from its center. To carry out the asymmetry, the ciliary body is usually shortened in the nasal quadrant, though sometimes the forward extension of the temporal portion of the retina restores practical uniformity of width to the ciliary zone in all meridians.

(C) Eye Movements and the Fovea

Kinds of Eye Movements—Except where the eyeball is practically microscopic (blind fishes, cave salamanders, etc.), the standard set of six oculorotatory muscles is always present, even in animals whose eyes might turn but never do, and even in those whose orbits are so snug that the eyes cannot be turned even passively. Most eyes, of course, can turn in their orbits; and their movements fall into a classification as follows:

Eye movements	Involuntary		Always coördinated, so as to appear conjugated. (In all vertebrates whose eyes are mobile at all).
	Spontaneous (voluntary)	Independent	With no coördination. (In most lizards and in birds).
			With coördination in convergence. (In some fishes and in chameleons).
		Conjugate	(In mammals exclusively).

Involuntary eye movements, in the sense implied here, are not necessarily either unconscious or incapable of being inhibited, but they are not willed movements made for the purpose of changing the visual field. Rather, they are automatic, reflex movements which are intended to keep the visual field as nearly constant as possible during locomotion and during passive jogglings of the head and body. In this class fall the various 'compensatory' and 'nystagmic' movements. An example *par excel-*

lence is the converse eye movement we make with each movement of the head when we shake it vigorously in the gesture of 'no'. Whenever this gesture is made in the course of a face-to-face conversation, we should find it most disagreeable if the image of the other person, and the whole visual field, oscillated with our head movements. If the reader will try to obtain this unpleasant experience by shaking his head without letting the eyes turn in their orbits, he will find some difficulty. The very act of fixation itself *seems* to set off any and all eye-muscle reflexes which are needed to compensate for head and body movements and maintain the status quo of the visual field.

Actually, the eye-movements of the 'no' gesture, and those made automatically when the head or body is turned actively or passively in any direction, have their origin in muscles of the neck and in the apparatus of dynamic equilibrium, in the membranous labyrinth of the internal ear. Disturbance of this apparatus will disturb the involuntary eye movements, as occurs in vertigo, intoxication, and in artificial situations such as caloric nystagmus—the induction of convection currents in the labyrinthine endolymph by the instillation of hot or cold water into the external auditory canal.

These involuntary eye movements in man and other vertebrates are invariably coördinated; that is, the movements of the two eyes are always in the same sense. If a fish turns sharply to the right, the two eyes rotate leftward, the right eye turning toward the snout and the left eye away from the snout. Though the eyes may move independently for the exploration of the visual field, it would never do for them to move unharmoniously if the field is to be kept as nearly constant as possible. Where this is actually impossible of accomplishment, the eyes will still try to hold on to the field, as in the 'optomotor reaction' so often elicited from laboratory animals for the study of their vision:

The animal is placed on a turntable, in the center of a cylinder coaxial therewith. The inside of this cylinder or drum bears a pattern, say, of vertical stripes. If either the cylinder or the turntable is rotated, the visual field is swept past the animal's eyes. If it is the turntable which rotates, the animal's labyrinths are naturally being stimulated and we should expect him to make compensatory movements of the eyes, head, body, or perhaps all three, in the opposite direction. If only the *drum* rotates, there is then no stimulation of the labyrinths; but still the eyes turn, in the direction the field is moving. This is the optokinetic or optomotor reaction. When the eyes have swung over as far as they can,

they may periodically jerk to the position of rest and repeat the slow following-movement. If the animal is one which has little or no eye mobility, the optomotor reaction will be given by the head itself or, if this be restrained, by the whole body. This reaction has been much used in late years (quite improperly!) as a test of visual acuity and as a tool for the investigation of color vision and still other matters—the assumption being that if the stripes are made so narrow or so much like the intervening spaces that the reaction fails to occur, the width of the stripes and spaces look alike to him however different they may look to us, etc.

We perform something essentially like the optomotor reaction, in our so-called railroad nystagmus. When watching out of the window of a swift train, we are comfortable enough if we look at distance objects, which seem hardly to move backward at all as we fly along. But if we try to watch the roadbed close beside the train we soon experience a discomfort—our eye muscles are in a turmoil, the eyes constantly jerking ahead and drifting back in a vain effort to stop the flight of the ties under the neighboring track.

Voluntary eye movements are those made for exploratory purposes. In ourselves, they are conjugated, which means something more than simply coördinated: we are quite incapable of voluntarily moving one eye independently of the other. The two eyes move together in both involuntary and voluntary movements, just as though there were a tie-rod inside the head like that which conjugates the front wheels of an automobile. There has been exactly one case reported, of a human being who could move either eye at will. This was a 28-year-old Australian, described by Sir James Barrett, who could turn either eye outward 20°, or both eyes at once—an amazing feat which he had always been able to do and which "came as natural to him as moving his hand." Our eyes always move in the same sense, in obedience to certain laws which govern the interactions of their muscles (Donders' and Listing's laws), for a change of fixation; but they move in opposite senses—toward or away from each other—for a change in accommodation. These contradictory tendencies are controlled from separate centers in the tegmentum, beneath the aqueduct of Sylvius (the convergent movements being commanded by a special center, the nucleus of Perlia); but they are smoothly blended without conflict whenever we turn our gaze to a new object which lies both in a new direction and at a new distance.

The system of involuntary and voluntary eye movements is subject to enormous differences from the human scheme of things, as is hinted in

the classification given above. These differences find their explanation in the presence and absence, and the location, of special retinal regions of particularly high resolving power. Table III (p. 187) lists these areæ and foveæ and should be constantly consulted while reading the ensuing discussion of eye movements in the various classes of vertebrates.

Fishes—The fishes reveal plainly that the original, primitive function of the eye muscles was not to aim the eye at objects at all. Their original actions were all reflex and involuntary, and were designed to give the eyeball the attributes of a gyroscopically-stabilized ship, for the purpose of maintaining a constancy of the visual field despite chance buffetings and twistings of the animal's body by water currents and so on. We will see later, when we consider the subject of movement-perception, just how and why this constancy of field is important.

The vast majority of fishes have only the reflex, involuntary, eye movements.* Except in such forms as the rays and flatfishes, these are chiefly in the horizontal plane. The bottom-hugging rays look mostly up and down rather than from side to side, and in them the superior and inferior rectus muscles are better developed than the lateral ones, whereas in their pelagic relatives the sharks, the lateral recti are the heavier. In fishes whose eyes sit laterally, every turn of the head is accompanied by a compensatory turning of the eyes. A moving object is never followed by an eye movement—instead, the fish (having, ordinarily, no neck) bends or turns the whole body so as to face the interesting object and keep it in the binocular field. In aquarium specimens, 'wheel' movements of the eyes can often be clearly observed: as the fish tilts his body in starting to swim upward or downward, the eyeball makes a compensatory rotation in the plane of its equator. This movement, obviously carried out by the two oblique muscles, suggests that this was the primitive function of those muscles.

In a number of species, spontaneous movements are known to occur. All of these forms which have undergone histological examination (except *Corydoras!*—see p. 387) have been found to be provided with a fovea, and there is an excellent correlation between the degree of perfection of the construction of the fovea—(in regard to visual-cell concentration, exclusion of rods, depth of depression, etc.) and the extent

*Retractive movements of the eyeball, which may perhaps be voluntary, are common enough in fishes and other vertebrates; but such movements have of course nothing to do with space-perception.

of the voluntary eye movements. A list of species known to have a fovea, compiled chiefly from the recent work of Kahmann, follows:

With good fovea:

Girella sp.	*Julis geofredi*
Hippocampus spp.	*Blennius basiliscus*
Siphonostoma typhle	*Blennius gattorugine*
Syngnathus acus	*Blennius sanguinolentis*
Syngnathus tenuirostris	*Blennius tentacularis*
Serranus cabrilla	*Blennius ocellaris*
Serranus hepatus	*Blennius pavo*
Serranus scriba	*Pholis gunellus*

With fovea, or at least the beginnings of one:

Balistes capriscus	*Trachinus vipera*
Balistapus aculeatus	*Julis vulgaris*
Tetrodon fluviatilis	*Julis pavo*
Trachinus draco	*Agonus cataphractus* (?)

These foveate fishes are all marine and inhabit the littoral zone. Some are characteristically agile and lively in the pursuit of prey, though others are sluggish, and the pipe-fishes and sea-horses have very deliberate swimming habits. Several of the species inhabit rocky clefts, where their capacity for eye movements seems a definite advantage in their cramped quarters. Rather surprisingly, considering its behavior, the archer-fish (*Toxotes jaculator*) is not among those which have a fovea; and it will be recalled (p. 292) that this fish also has a rather narrow binocular field.

In all of the above species except the sea-horses, the fovea is located strongly temporally, in the retinal region which can see binocularly (Fig. 77b, p. 185). But while these fishes can and do converge their eyes to aim both foveæ at a prey object, the eyes are moved independently and are not conjugated, but only coördinated temporarily in each act of convergence. In fact, such fishes are the only vertebrates which can employ a temporal fovea for monocular vision. In such genera as *Blennius, Serranus, Julis,* and *Trachinus,* either monocular or binocular fixation may be maintained on an object. The better the fovea, the greater the tendency to adhere to binocular fixation. The average teleostean fovea is a shallow pit, far inferior in construction to sauropsidan foveæ; but in *Girella,* according to Mlle. Verrier, it is the equal of the superb fovea of the chameleons. Some syngnathids have been claimed to have two foveæ in each eye, but Kahmann was unable to confirm this.

Many other species, among those kept in large American aquariums, can be seen to make spontaneous fixative movements. Most of these have

a prominent aphakic space (Fig. 105f, p. 261)—so commonly associated with a temporal fovea—and all of them should be studied histologically. Examples are: *Promicrops itaira, Stenotomus versicolor, Monacanthus ciliatus, Centropristes striatus, Mycteroperca bonaci, Sphæroides maculatus.*

The fishes thus illustrate clearly the universal principle that: *where there is no fovea, or at least a well-defined area of acute vision, there are no spontaneous eye movements.* For, unless one spot of the retina is clearly superior to the rest in resolving power, there is no advantage in aiming any one part of the retina at the object of interest, whether the latter is still or in motion. Only when the object has moved close to the edge of the visual field will any action be taken to maintain visibility of it—and then it is by a turning movement of the whole body (or of the head if a neck is present), and not by a movement of the eye unless the optomotor reaction is being evoked. The act of precise *fixation,* then, is performed only by areate and foveate animals.

Amphibians—No amphibian is known to perform any eye movements other than retraction and elevation. Since retraction is usually, if not always, elicited by a contact with the eye or used (by the Anura) as an aid to swallowing, it is questionable whether it is ever spontaneous. In turntable experiments, amphibians exhibit the usual compensatory movements and also give an optomotor reaction to a rotating field; but in the absence of a neck (anurans) these movements are of the whole body. The eyes do not turn in the orbits at all. Frogs have an area centralis, but this is a large, vaguely defined, horizontal crescent (in *Hyla,* a large circle), whose superiority in resolving power, over the remainder of the retina, is extremely slight. There is therefore no more need of any fixative aiming of the eye than in the great majority of fishes.

Reptiles—Reptiles may sit for hours without making spontaneous eye movements; but most species are capable of them, as well as of the full panoply of labyrinthine and optomotor reflexes involved in the gyroscopic maintenance of the visual field.

The crocodilians have not been much studied; but, being nocturnal, they are probably comparable to the amphibians in the matter of eye movements. The turtles however, despite the absence of a fovea in all but *Amyda,* have a good-enough area centralis to need the power of fixation. Their lateral eye movements, particularly in carnivorous forms, are coördinated for binocular observation; but vertical motions are made independently by the two eyes, which are thus not truly conjugated.

In *Sphenodon,* and in the lizards except the monitors, the binocular field is so small, and the fovea so nearly central, that any binocular employment of the fovea (such as can occur in some fishes) is out of the question. Lizards on the whole rely entirely upon monocular fixation, with the two eyes wholly independent in their voluntary movements. Monocular fixative and exploratory movements are especially conspicuous in alert and active lizards such as the agamids, iguanids, and *Zonurus.* But independent spontaneous movements of the eyes reach their zenith in the chameleons (which are so frequently stated to be the *only* vertebrates whose eyes move independently). The extraordinary mobility of the chameleon eye is the resultant of several factors: the lid crater around the small cornea restricts the external visual field of the eye; the visual axis is long and the retinal image relatively large; and the retina, away from the fovea, falls off rapidly in quality of construction for high resolving power. The insectivorous feeding habit, in so slow-moving an animal, requires perfect judgment of distance, necessitating that the eyes be capable of enough convergence to give the foveæ a common point of aim. The chameleon's eye bulges quite a bit from the head, enabling the animal to sweep the visual line through a wide angle, turret-fashion; and it can employ the eyes independently for its perpetual exploration of the surroundings or, at will, associate them for foveal binocularity when a prey insect is spotted. The eye can be turned through 180° horizontally, 90° vertically, and one eye may be made to aim backward while the other looks straight forward. By way of comparison, *Lacerta viridis* (a typical lizard) has but 40° of eye movement.

We have seen that only the teleosts can use a *temporal* fovea *monocularly.* The chameleon is also exceptional, in that it can use a *central* fovea *binocularly.* The movements of its body are slow in the extreme—reminding one of the sea-horses (which also have central foveæ and prehensile tails, and better deserve to be called the 'chameleons of the sea' than other fishes which have been given that appellation)—but the sticky tongue is shot out with lightning speed at any insect that settles within range. As Rochon-Duvigneaud has so well put it: "S'il y a encore des caméléons, c'est que leur oeil est infaillible."

Many of the more sluggish, less eye-minded lizards, such as the Gila monster, have fixed eyes; and in the snakes there is but little spontaneous mobility. It is because of this that the static binocular field of snakes is wider than that of the lizards whose eyes can move and converge. What movements the snake's eyes do make are either independent or, in con-

vergence, simultaneous. Like the turtles, the snakes prefer to scrutinize objects binocularly, and even those whose binocular fields are narrow will move the head from side to side in pendulum fashion, as if they were trying the impossible of seeing all of the object with both eyes at once. *Dryophis* and *Thelotornis,* probably *Dryophiops* as well, have temporal foveæ and enjoy foveal binocularity without benefit of convergent eye movements (see pp. 185-6, 299).

Birds, and the Visual Trident—For reasons which were pointed out in Chapter 8, the bird eye is even larger than that of a lizard. It is a very tight fit for its orbit, which could be called roomy only in the penguins and cormorants. Only these birds, some other divers such as the pelicans and gulls (and, strangely enough, the hornbills and ground hornbills) have much eye mobility. Most birds have little or no spontaneous mobility, relying upon the flexibility of the neck; and even the reflex eye movements may be greatly restricted and replaced by reflex neck movements. In some cases, the eyes can turn reflexly in the vertical plane but not when the head is rotated in the horizontal plane. Moving objects are generally followed by movements of the whole head. Fixation may be monocular with the central fovea, or binocular for optimal judgment of distance—even in parrots, whose binocular field is very narrow. Such spontaneous mobility as there may be is mostly horizontal, and for the enlargement of the binocular field. Even the hen is capable of this slight convergence, despite a 144° divergence of the optic axes.

The imperative need for accurate distance-judgement, coupled with the impossibility of any chameleon-like binocular use of the central foveæ, has led to specializations of the temporal part of the retina. Some of these are slight, like the 'red field' of the hen; but in many different groups of birds, independently of each other, a second fovea has been differentiated in the temporal quadrant. It is present in the very birds which, one might say from their feeding habits, need it most: the various hawks and eagles, the humming-birds (Fig. 80b, p. 188), the swallows, many bitterns, and various passerine wing-feeders. Despite their close kinship with the hawks, the vultures apparently lack the temporal fovea. Since they are ground feeders, this is readily comprehensible. The extra fovea of the kingfisher is believed to have a very special significance (see p. 442).

The accipitrine birds, the swallows, etc., thus have what Rochon-Duvigneaud has called the 'visual trident'. They look antero-laterally

with the two central foveæ, and binocularly straight ahead with the two temporal foveæ (Figs. 114, 115). A substantial part of the whole visual field of the bird is thus subtended by highly superior receptor areas. The sacrifice of lateral and posterior visual field entailed by the frontality of the eyes is easily made by the hawk (which fears no enemy whether he can see it approach or not) and by the swallow, which expects to outfly any challenger.

Except in the eagles and in *Apus apus,* the temporal foveæ are inferior in construction to the central ones. This seems to hint that in birds (unlike ourselves) binocular resolving power is higher than monocular

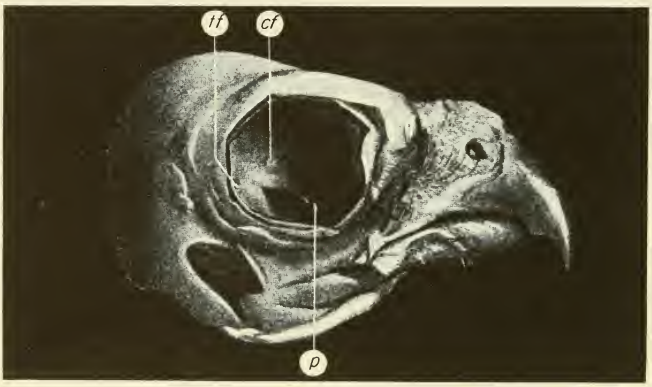

Fig. 114—Dissected head of a hawk, with eye bisected equatorially. After Rochon-Duvigneaud. *cf*- central (nasal) fovea; *tf*- temporal fovea; *p*- pecten.

—being teamed with its mate in the other eye, the temporal fovea perhaps does not need the structure of the central one which works alone. A hawk prefers to turn the head to follow objects binocularly, and can rotate the head on the neck through a full half-circle. But if the head is held, the hawk will 'follow' monocularly within the narrow limits of its ability to swing the eye in the orbit.

The owls have only the temporal fovea. It is an academic question whether this was once a second fovea and the original, central one has disappeared, or whether a one-and-only fovea migrated temporally as the eyes became more and more frontally aimed, during the evolution of the

owls from swift-like forms through the goatsucker and frogmouth types. The situation in *Apus* (p. 188) suggests that the ancestors of the owls may have had both foveæ. A central fovea would be of little value to a modern owl; for, owing to the great restriction of the visual angle in the tubular eye, the angle between its line of sight and that of the temporal fovea would be a narrow one. The owl eye cannot be turned in the orbit, even with a pair of pliers. It has been pointed out that these, the most frontal of all bird eyes, are the least mobile while the most frontal of all mammalian eyes (our own) are the most mobile. This makes sense how-

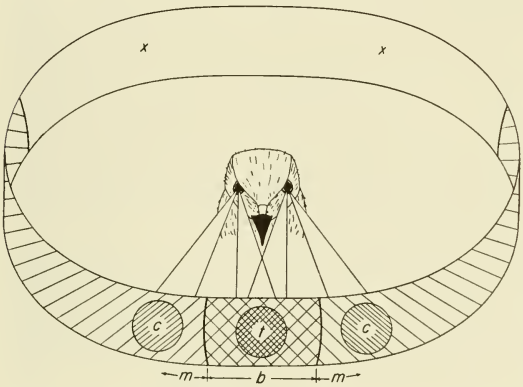

Fig. 115—Projections of the visual fields of a hawk, showing the visual trident of bifoveate birds. Relative resolving powers are suggested by the closeness of the hatching. *b*- binocular field; *m, m*- residual monocular (uniocular) fields; *x, x*- blind region; *c, c*- projections of the central foveæ; *t*- common projection of the temporal foveæ.

Fig. 116 — A bittern, *Ixobrychus minutus,* in 'freezing' posture, showing ability to see binocularly beneath the head. Redrawn from a photo in *LIFE.*

ever when it is kept in mind that the owl's head can swivel through 270° or more; and this situation actually does have its parallel among the primates—in *Tarsius,* whose tubular eyes are immobile and whose head can rotate on the neck through an angle of 180°.

The owl is safe enough in the matter of distance-estimation, without having a visual trident—for it does have the all-important central tine of the trident; and its almost bat-like ability to dodge obstacles, through the use of auditory cues, enables it to avoid crashes as easily as does a hawk. But the necessity of the temporal foveæ (with or without the rest of the

trident) for perfect judgment of the distances of objects has been brought out experimentally in the interesting experiments of Portier on the Northern gannet, *Morus bassana*. This bird has only central foveæ and is one of the many fish-eaters which dive after their prey. Such birds, plunging into yielding water with the beak open or with talons spread, have only to continue in the right direction to seize their fish—they need not have good judgment of distance. A falcon, however, stooping for a rabbit, must know where and when to check its flight or else collide disastrously with the ground. To study the gannet's ability to do this, Portier fastened fish on top of floating bits of board and then rowed away to let the birds get a good look. He found that the gannets, diving upon the fish bait, could not tell where to stop and would even transfix the soft wood with their beaks, thus trapping themselves. This bird—often called 'booby'—may not be able to learn much; but the falcon is not given a chance to *learn* that the hard earth will kill him. He must have the equipment for distance-estimation ready-made, and use it instinctively. The gannet, not being similarly equipped with the complete foveal trident, could never have mastered the problem Portier set for him, even if he were far more intelligent than he is.

Clearly, the central foveæ are of no value in binocular distance-judgment, but are of use to the flying bird only for seeing and avoiding obstacles while the temporal foveæ are kept aimed straight ahead. Birds in flight are commonly observed to tilt the head on one side to look down to the ground monocularly; and this is as true of those provided with the visual trident as of those which have only central foveæ.

Mammals—In the matter of eye movements, the mammals are at once set off from all other vertebrates by the fact that whenever voluntary movements are possible at all, the two eyes are never independent but are always conjugated.

This universal conjugation is associated with the fact that mammals (whales, rabbits, and some others excepted) examine things only binocularly—even the bats, small rodents, insectivores, and other nose- or ear-minded nocturnal forms whose eyes never move even reflexly. Where the eyes are placed laterally as in the rabbits, there is usually no area centralis, let alone a fovea, and there are no spontaneous movements at all. But even the rabbits have the gyroscopic reflex eye movements, including the optomotor reaction. These compensatory movements in mammals are always most extensive in the plane of greatest biological usefulness, which

usually means horizontal. The hippopotamus, lying with the eyes just out of water, is claimed by one author to be able to make even voluntary, monocular, vertical movements like a sauropsidan. The modern hippopotamus has no aërial enemies, or indeed any known enemies at all; so the value of this 'ability,' if it exists, is doubtful. It may be a necessity, rather than an ability—imposed by the slender horizontal pupil.

Where the angle of eye movement is small, the lid opening is also small. One can thus judge the extent of ocular mobility in a given mammal by noting how much of the white of the eye (the sclera) shows. Spontaneous eye mobility is greatest in the higher primates, which alone among mammals have a fovea; but even here it is supplemented to a surprising degree by head movements, as we soon find out when we spend a day with a stiff neck. It is next-best developed in the larger carnivores, particularly the cat and dog families; but it is not so conspicuous in the ungulates. It is probably only accidental that voluntary eye movement seems best developed in the 'most intelligent' mammals, as has been pointed out by some authors. The elephant, with high intelligence and little eye movement, seems to be the exception which destroys the rule.

The voluntary eye movements of mammals are really best correlated with visual acuity, which, it so happens, does go pretty well with intelligence in this group of vertebrates. The mammals obey the rule that such movements occur only where there is a fovea or a circumscribed and distinct area centralis. Binocular employment of the two areas (in primates, the two foveas) is so valuable and so constant that it has become fixed in the neuromuscular apparatus as an unlearned habit, the expression of which is the continuous conjugation of the two eyes—so different from the mere temporary coördination of a fish or a chameleon. Again, the urge toward binocular vision has operated in evolution to increase the degree of frontality in the most eye-minded of mammals—the primates and the larger carnivores and ungulates. In the individual mammal, even, the urge to see binocularly is extremely powerful. Even in animals for which it is a great labor, the head is turned to face squarely an object which has taken the attention. Thus the horse, for example, fixates objects binocularly until they approach within three or four feet, when he is forced to turn his head away and continue his observations monocularly. In cats and dogs, if the insertions of the superior rectus and external rectus muscles are surgically interchanged, or even if the external is removed and the superior brought down into its place, the eye movements become completely re-conjugated in a few days. Recent work

on monkeys has shown that all four recti can be shifted about, the eyes becoming re-conjugated in a few days.* The recovery takes place, though more slowly, even when the animal is kept in darkness.

It is the predator which visually pursues its prey, and the inquisitive primate picking up this object and that for manipulation at close range, which have the greatest need for the accurate estimation of distance which sharp binocular vision alone confers. Such vision is obviously aided as much by frontality as by the improvement of the area and the final creation of a fovea. According to Lindsay Johnson and Elliott Smith, no non-simian mammal can converge its eyes, though it is perhaps significant that cats and dogs can be taught to do so—the cat being perhaps closer to the verge of producing a fovea than other arhythmic mammals. Nicolas, however, states that the dog converges naturally. Other authors have claimed that many mammals do converge when excited in the pursuit of prey or in fleeing from an enemy, thus widening the binocular field when it will do the most good. Such convergence is not necessarily *voluntary,* however. Even in the rabbit, which has no voluntary eye movements, the angle between the optic axes is less when the animal is excited than when it is undisturbed (see Table X, p. 298).

The squirrels, and especially the marmots with their 'universal macularity', constitute a rather special and interesting case. The marmot or prairie-dog's eyes are strongly lateral and are but slightly movable. But the retina has everywhere as high a resolving power as many another animal's fovea, so there is no need of fixative, aiming movements of the eyes. As Rochon-Duvigneaud has pointed out, the marmot can explore space without betraying itself by the slightest movement, even of its eyes. It is thus far from being in the same class with such forms as the rat or the frog. The latter keep their eyes still not because their retinal resolution is everywhere so excellent, but because it is everywhere so poor.

The case of the marmot is the only one which prevents us from generalizing that the spontaneous eye motility of vertebrates is correlated with high visual acuity as such. We still must say that such movements occur only where there is high acuity of vision within a restricted area of the retina (p. 305), which must be directed toward an object if the latter is to be seen at all well.

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*The investigators (Leinfelder and Black) found however that if the superior oblique was disturbed there was no re-coördination even after months. The meaning of this is not yet clear.

(D) Depth- and Solidity-Perception

In the first section of this chapter we considered the methods by which vertebrate eyes adjust themselves for the distance of the object being viewed. It was pointed out that this adjustment, accommodation, has nothing to do with giving the animal an awareness and estimate of the distance. This awareness of the 'third dimension', or toward-and-away distances and movements, is a perceptual matter and not, like accommodation, an optical one. Moreover, it is unrelated to the perception of movements in the other two dimensions of space—horizontal and vertical displacements of visual objects. This latter kind of perception, which is movement-perception in the usual sense of the term, is considered in the next section. Here, we are concerned with the means by which man and animals judge visually the distances, depth, and thickness of objects; and with the question of whether, and how, vertebrates perceive solidity—whether, for any of them, stereopsis is possible as it is for man.

Clues to Depth and Distance—The estimation of distance is an exclusive monopoly of the sense of sight in all vertebrates except the bats. It is quite impossible to be sure of distances when walking in the dark, and our judgment of the distance from which a sound has come is faulty in the extreme. In human vision, a number of clues exist which we integrate perceptually to arrive at an evaluation of distance and the relative distances of several objects. Most of these clues are as readily employed in monocular vision as in binocular—in fact, they are incorporated by any good artist into his two-dimensional painting in order to promote the illusion of depth (see also p. 194). But when the two eyes are in use in a three-dimensional visual field, a special and important factor is introduced which is of particular value when the object is close at hand; and, of course, it is the closest objects which are most important visually, as any blind man knows. There is no more vexed question in all of comparative ophthalmology than the one whether this binocular factor in depth-perception exists for vertebrates below the mammals. But certainly the same *monocular* clues that we humans employ are available to all vertebrates. Whether a given animal can use a particular one of them, however, depends upon his powers of observation, his learning capacity, and his equipment of instincts. These monocular clues are:

A. Retinal image size. Where the object is a familiar one, its apparent size, as determined by the size of its image on the retina, is a cue to its

distance. As an object approaches, it appears to grow. A closely related cue is:

B. Perspective. All horizontal lines, if produced, appear to meet at the horizon. An object appears farther away if its horizontal contours are close to meeting. We know which end of an object is nearer to us, from the direction in which the object appears to taper.

C. Overlap and Shadow. If one object hides part of a second object, it must be the nearer of the two. So also if it casts a shadow on the second object. The more overlaps there are in a visual field, the greater seems to be the distance to the farthest object. This is why distances over water, with no intervening objects, tend to be underestimated.

D. Vertical Nearness to the Horizon. When we are looking at nearby objects, our line of sight tilts toward the ground. More distant objects are seen at apparently higher levels, for in looking at them the line of sight must be elevated.

E. Aërial Perspective. Objects appear farther away if their outlines are hazy and their surfaces dim or bluish, for long atmospheric pathways create such appearances. Colors are affected by aërial perspective and become unsaturated at a distance. Distances through exceptionally clear air tend to be underestimated; distances through mist, overestimated.

F. Parallax. This, the most important of all monocular factors, is the change in the apparent angle, at the eye, between a near and a far object, produced by a lateral movement of the observer's body or head. As we move our heads from side to side, near objects seem to move extensively in the opposite direction as compared with far objects, while the latter seem to move slightly, in the *same* sense as the head movements, in relation to the nearer objects. It is chiefly this cue which enables a one-eyed man to move about in an unfamiliar roomful of furniture without bumping into things any more often than a two-eyed person.

The one-eyed person, however, may have considerable difficulty with the common parlor trick in which one attempts to bring two pencil-points together with the arms outstretched. Binocular perception of distance—short distance, at any rate—is infinitely finer than monocular. What is its special basis?

In binocular vision, whenever the eyes accommodate for a particular distance, they also converge to a degree that aims the two foveal lines of sight at a common point at that distance. In looking from one object to another which is at a different distance, the extent of convergence either

increases or decreases. The amount of convergence, evaluated quite unconsciously *via* kinæsthetic reception from the internal rectus muscles, is a potent cue to distance. It is effective up to the greatest distances for which we converge at all appreciably—up to a hundred feet or more, which is far beyond the distances for which we accommodate.

The stimulus to converge seems to be the psychic impression of nearness. Convergence is then guided to the point of precision by the urge to unify the two one-eyed images of the object being attended to, with accommodation tagging along as a dependent reflex. When the object is seen singly, convergence and accommodation freeze; and the parallactic angles of convergence of the two eyes, being simultaneously recorded in the nervous system, afford a precision of distance-judgment which successive monocular parallaxes can never yield. The perception of singleness is inseparable from the perception of the distance of the object; and in fact both are *attributed* to the object—the latter's distance from us seeming as much a part of the object as its size and shape. In man, at least, singleness of a solid object is also inseparable from the perception of its solidity—the psychic process which we call stereopsis.

Stereopsis in Man—Stereopsis means, literally, 'seeing solid'. As a word, it has been loosely used as a synonym for distance- or depth-perception (which is better known as bathopsis); but we can perceive depth without solidity, or solidity without depth. For the estimation of distances in the visual field, convergence must be allowed; and it must be allowed to 'play' or vary back and forth until it finds its dead center on the object. But the perception of solidity is literally lightning fast, for it is obtained in a stereoscope even when the pictures are illuminated by a single electric spark lasting a ten-thousandth of a second. This, 'Dove's experiment', is conclusive evidence that solidity does not depend upon a play of convergence, for no time is allowed for that process. Nor is convergence as such even necessary, for prisms can take its place as they do in the ordinary stereoscope. As Javal pointed out years ago, the *idea* of relief is one thing, and its *measurement* is another. Estimation of distance, depth, and thickness is closely associated with the recognition of solidness, for both involve the idea of tridimensionality; but the one process is dynamic and the other, static.

For stereopsis, the prime essential is a particular blend of likeness and difference between the images on the two retinæ, and a particular position of each image, this position being governed in ordinary experience by the degree of convergence. But it does not really matter what the positions

of the eyes happen to be, if only the retinal images are of the right kind and in the right places, even if put there by an arrangement of prisms or mirrors in an experimental situation.

The two retinal images must either be left- and right-eyed views of an actual object or, in the case of drawings which are to be observed in a stereoscope (Fig. 117) they must represent such views of some possible solid object—even if it be an imaginary geometrical figure or a gimmick the like of which the observer has never seen. The two single-eyed views of a solid object can never be identical even if the object is a smooth ball —unless it is so lighted that it has no shadow which can be seen more

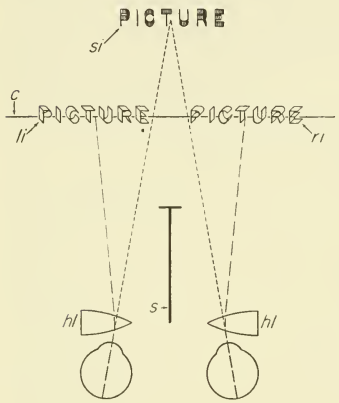

Fig. 117—Optics of the Brewster-Holmes stereoscope.

A card, *c*, bearing a left-eyed image *li* and a right-eyed image *ri* of some three-dimensional scene, is observed through the half-lenses *hl*, whose prism action so bends the light rays that the retinal images are projected to a common place in space for which the eyes are converged and accommodated. At this place, a binocular stereoscopic image *si* is seen. The screen *s* prevents each eye from seeing the picture not intended for it.

fully by one eye than by the other. Yet any two pictures placed in a stereoscope must be as nearly identical as right- and left-eyed views are, or they cannot be 'fused' and will be seen doubly or even alternately by the baffled brain, in the phenomenon mis-called retinal rivalry.

The left eye sees a little way around one side of an object, the right eye a little way around the other. Naturally enough, if these two images are fused at all into a single central or cerebral image, the rotundity of the object is perceived. Of course if the object is two-dimensional, it will be perceived as such; but even so it will be seen singly, through the fusion of two one-eyed images. Here, no third dimension is created, not because the object hasn't one but because the two retinal images in this

case are absolutely identical.* An approach to this situation is obtained when we look at objects farther and farther away. We can judge their distances binocularly, with convergence as the chief clue, up to about one hundred feet; but even far short of that distance all solidity—where it really depends upon disparate retinal images and not upon our familiarity with the object—is lost. Such distant objects appear flat simply because, with the lines of sight making so slight an angle with each other, the two images we have of the object are not different enough to yield any rotundity when fused.

Stereopsis, then, results from the fusion or unification of two views which differ slightly in a particular way and within certain limits. The object must be seen singly, and this is where the matter of the location of the images on the two retinæ comes in:

The two images of any object-point must fall upon 'corresponding points' of the two retinæ if they are to be fused. The two foveæ are corresponding points, and if identical small images are falling upon them, no matter whether they emanate from a single object or not and no matter in what direction each eye is pointing, those images will be fused.

When a point at any given distance is fixated by both eyes and is seen singly, there is at the same instant an infinity of other points in space which are seen singly along with it. Their images are falling upon corresponding retinal points other than the foveæ; and the external, spatial points themselves determine a complexly shaped hypothetical surface hanging out in space, called the horopter. There is a different horoptral surface for every point of binocular fixation, at every distance and direction. Obviously, the whole matter of horopters can become hideously complicated, and it is as well for the reader (and the writer!) that we shall not need to worry much more about them. Suffice it to say that when you fixate a point across the room, and raise a finger into the line of fire, you see the finger doubled, because the right- and left-eyed images of it are not falling upon points in one retina which 'correspond' with the stimulated points in the other. They could be made to do so if the finger were amputated and carried out and glued onto the horopter-of-the-moment. But by merely *looking* at the finger the two images are made to slide together into one, for the change of convergence and accommodation has created a new horopter on which the finger now lies.

*Unless the object is quite small and quite near—say, a calling-card at the near point—when the images are of course appreciably 'keystoned': for each eye, the card tapers in the direction of the other eye.

These doubled images are a sign that the object is not at the distance of accommodation-and-convergence, and their appearance and disappearance (though we are ordinarily totally unaware of them) is a minor binocular cue to distance. Another kind of double vision also demonstrates, and more dramatically, our dependence upon corresponding points: If one eyeball is pressed and wiggled by a finger placed against the lower lid, the image on its retina is displaced from the set of points corresponding to those under the image in the other eye, and the visual field seems to split and become two fields, one of which slides around over the other as the finger is wiggled. We can unify the two fields only by allowing the eye to go back into its natural position, which is one in which corresponding points are stimulated by the object upon which the attention is fixed. Even Barrett's Australian patient (*v.s.*) with his remarkable ability to dissociate the two eyes at will, had continuous 'diplopia' or double vision while doing so.

Diplopia is simply the seeing of one object in two directions at once. Each point on each retina has its 'local sign' of direction. To take the centralmost point for example: when this point receives the image of an object, the brain sees that object in the direction in which, so to say, the brain thinks the eye is aimed. Having given the neck muscles and the extra-ocular muscles certain orders, the brain thinks it knows where the eye is pointing. But if we move the eyeball passively, with a finger-tip, the brain is deceived—the object in space has not moved, but it is now imaged on a different spot on the retina which has a different local sign of direction. *This* spot is now actually aimed along the same straightforward line in which the fovea was pointing a moment ago. The brain does not know this, for the muscles have not been told to turn the eye. So, the brain sees the object in a new direction, different from that in which it is seeing it with the other, undisturbed eye. This new, second direction *is the one in which the object would have to lie to be imaged where it is on the retina, if the fovea were still pointing dead ahead.*

Now, if both cerebral hemispheres, looking through both eyes, are to see a single object at the same place in space—fuse it, in other words—the object must be imaged upon corresponding points in the two retinæ. This is only another way of saying that the two retinal areas receiving images of the object must have the same local sign of direction. Whence arise these all-important corresponding points of the retinæ—which, except for the foveæ themselves, are no fixed anatomical points at all, but pair up in ever-shifting combinations as the fixation is aimed here

and there in space? The traditional explanation of them is based upon a certain peculiarity of the mammalian optic nerves:

The Optic Chiasma in Man and Other Vertebrates—In the vertebrates the optic nerves from the two eyes never enter directly the respective sides of the brain. Instead, they come together beneath the brain and cross over or through each other in an x-shaped structure called the optic chiasma (Figs. 21, 70; pp. 47, 172). From this, they continue to the brain as the 'optic tracts'. In all vertebrates from the lampreys to the birds inclusive, all of the optic nerve fibers from one eye cross over in the chiasma to form the optic tract of the other side, so that each eye is connected only with the opposite half of the brain. This is called 'total decussation'. Similar decussations are very numerous among the fiber tracts of the spinal cord and brain stem, and there is no discernible reason for any of them—they apparently just happened in embryos during the early evolution of the vertebrates, and became genetically fixed in the group. A vague sort of case might be made out for having the primitive vertebrate's left eye connected with the part of the central nervous system which controls the muscles of the right side, for these would be most important in turning the animal to face a light coming from the left. But, the left eye is connected with the right brain which owing to decussations in the motor tracts, controls the muscles of the left side. If we stick to our teleological guns, we are then forced to believe that the first vertebrates were negatively phototropic, which is most improbable.

In the optic chiasma of the mammals, and only in the mammals, an important modification occurs. In these animals the decussation of the optic nerves is partial: some of the afferent fibers from each retina fail to cross over, and hence enter the optic tract on that same side. In man, the proportion is just about fifty per cent, with half of the macular fibers as well as half of the extra-macular ones remaining uncrossed (Fig. 21a). The fibers from the nasal half of each retina are the only ones which decussate; and although there is no visible evidence of it, there is a vertical line neatly bisecting each human retina, which is the boundary between the retinal area connected with the same side of the brain and that connected with the other side.

In all mammals, the relative number of uncrossed fibers is closely proportional to the degree of frontality. It is about one-eighth to one-sixth of the whole in the horse, one-fifth in the rat and in the common opossum, one-fourth in the dog and the Australian bushy-tail opossum (*Trichosurus vulpecula*), one-third in the cat, and reaches a maximum of

50% in the higher primates and a low minimum in lateral-eyed forms; but even the rabbits have some uncrossed fibers. This relationship is the 'law of Newton-Müller-Gudden', and holds good only for the mammals. Outside of that class, there is no case of a partial decussation of any degree whatever.

Supposed Value of Partial Decussation—A few have thought that partial decussation arose as a device for preserving, in animals with frontal or partly frontal eyes, the original status in which the left brain saw everything that was to the right of the animal and the right brain

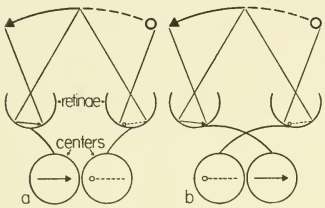

Fig. 118—Illustrating Ramon y Cajal's explanation of the decussation of the optic nerves. a, situation which would obtain if the nerves did not decussate: the two halves of the visual field are transposed. b, the decussation of the nerves makes the subjective visual field a proper panorama.

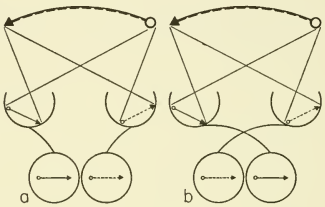

Fig. 119—Illustrating Ovio's correction of Ramon y Cajal's view: since the *whole* extent of any object in the binocular field is seen by each eye, and since the separate mental images are due to be fused interhemispherically anyway, it makes no difference whether the nerves decussate or not. a, without decussation. b, with it.

(In Figs. 118-121, the left- and right-eyed aspects of the visual field are respectively indicated by the solid and dotted portions of the visual object [arrow]).

kept watch on the left—the situation which obtains in a lamprey, for example, where there is total decussation and no binocular field at all. But this naïve view presupposes that the ancient invention of total decussation was somehow of vital importance in the first place; and, still worse, it rides rough-shod over the fact that Gudden's law is inoperable in lower groups despite the presence in them of species with even total frontality (some deep-sea fishes, owls, and—dynamically—chameleons).

The great majority of physiological opticists have instead seen in partial decussation the essential basis of fusion and stereopsis. The argument is that since there are no median end-stations in the brain, fusion must occur on each side and can only do so if each half of the brain

receives information from both eyes. This ignores the fact that what reaches each side of the brain is a somewhat lateral view of the object from the temporal half of one retina and a nearly straight-on view of the object from the nasal half of the other retina. If any combination of images in one side of the brain is essential for fusion, it would seem more logical for evolution to have produced a type of partial decussation in which the nasal halves of both retinæ were brought to one cerebral hemisphere and the temporal halves to the other.

The conviction that: "no partial decussation, no fusion" has led to some rather ludicrous corollaries whenever the convincees have been

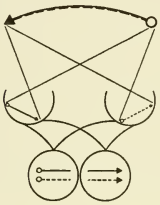

Fig. 120—Ovio's interpretation of partial decussation. The mental image is 'larger (therefore better resolved)' than where decussation is total (compare Fig. 119b).

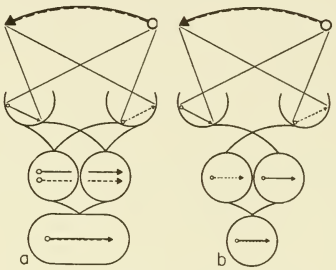

Fig. 121—Completion of Fig 120 (in a) and Fig. 119b (in b) by the addition of the psychic act of inter-hemispheric fusion, showing that with either partial (a) or total (b) decussation, the resulting fusion-image is of the same character (except for Ovio's difference in 'size', which is here allowed for the sake of argument).

made to face the situation in the non-mammals, with their indisputable urge to attain binocularity despite their total decussations. It is intolerable for us to observe, centrally, two totally different, unfusible visual patterns with the two eyes independently. Retinal rivalry at once sets in (see Fig. 122, p. 332) and a severe discomfort—powerful headache, or worse—rapidly develops. Having this in mind, it was impossible for the psychologist Wundt to imagine how a lateral-eyed animal, such as a fish or lizard, could possibly attend simultaneously to its two independent visual fields. Wundt believed that consciousness must alternate between them! Yet, we can give ourselves something like the effect of total decussation by simply pressing the upright hand flat against the nose. Each

eye then sees only fields in which the other eye can never see anyway, and the crescentic uniocular temporal retinal fields involved are totally decussated. Still, we are perfectly able to observe 'out of the corners' of our two eyes simultaneously. There is no alternation, no rivalry, no attempt to fuse and discomfort from its failure.

The great Spanish neurologist Ramon y Cajal believed that in forms with total decussation there must be panoramic vision, the visual fields of the two eyes being subjoined to complete the whole picture of space (Fig. 118). Without total decussation, he argued, the two halves of the whole field would be transposed in the animal's mind (Fig. 118a) and vision would become worse than useless for purposes of spatial localization and orientation. He thought that where there is partial decussation, fibers coming from corresponding points in the two retinæ ended up at single points in the visual cortex, in 'isodynamic cells' which accomplished the fusion. This theory might seem reasonable enough where the foveæ are concerned; but all other 'corresponding points' are impermanent and it would take an infinity of isodynamic cells to tie together all possible combinations of them. The whole matter of corresponding points is a psychological one, and not anatomical in any way, as the phenomenon of the substitute macula (*v.i.*) clearly shows.

Ovio has corrected Ramon y Cajal's idea of the panorama, which was based of course on the mistaken belief that a binocular field is an exception rather than the rule among vertebrates. Ovio's diagrams (Figs. 119a and 119b) bring out how little difference it makes to binocular vision whether there is total decussation or no decussation at all. Ovio believes that fusion (by superposition, not by continuity) takes place in animals with total decussation, since psychic fusion is a joining of the images in the *two* hemispheres into one phenomenally median image; but he goes on (Fig. 120) to explain partial decussation as a device for making the *mental* image larger, and 'therefore' better resolved. On this point, his reasoning becomes very hard to follow.

Ovio believes, with others, that solidity results from bringing together two disparate views of the object in the same center—*i.e.* one side (either side) of the brain—but that a 'psychic act' is still necessary to fuse them into a single solid image. The psychic act of fusion does not in itself create the relief, however; for even when we have only one eye open, that eye is evoking activity in both cerebral hemispheres and these two cerebral actions are being somehow unified, yet there is no resultant idea of relief.

If a fusion of right- and left-eyed images in itself creates the impression of solidity, then the question of whether total-decussation animals have stereopsis or not hangs simply upon the question: do they have singleness of vision in the binocular field? For if we complete either Figure 120 or Figure 119b by indicating the psychic act of fusion we derive Figures 121a and b respectively; and in them it would seem that the final result is the same—the fusion of the whole right-eyed view of the object with the whole left-eyed view. Even if we close one eye, we are still seeing with both halves of the brain. We still effect a junction of these bilateral activities. There is no reason why a fish cannot do likewise. The fusibility of images in the two sides of the brain into a 'median' image cannot conceivably depend upon the character of the optic chiasma.

If solidity crops out phenomenally in the case represented in Figure 121a, why not also in the case of total decussation shown in Figure 121b? If stereopsis depends only upon the fusion of the right kind of images, and we find reason to believe that animals with total decussation do have fusion and singleness in their binocular fields, then (since we know their images are of the right kind—*i.e.,* right- and left-eyed) we must look for an explanation of partial decussation other than the firmly-rooted traditional one that without partial decussation there could be no fusion and hence no stereopsis.

The Case for Singleness in Animals—Let us consider a fish, which of course has total decussation and which we will suppose to have no binocular field at all. He sees a mouse on the bank. He can look at the mouse with one eye, or turn his body and look at it with the other. In either case he certainly sees but one mouse, and he has no binocular parallactic cue to its distance and no impression of its solidity other than that afforded by monocular cues. But now an owl, who also has total decussation but who moreover has a wide binocular field and convergent foveal lines of sight, also looks at the mouse. Is it reasonable to suppose that the owl sees *two* mice? If so, must he aim his talons half-way between the two 'mice' in order to seize THE mouse—or if not, which 'mouse' shall he aim for?

Eye-minded species have certainly done everything they could do to gain binocular vision, by making evolutionary modifications of their static facial and ocular anatomy. Quite apart from the enormous aid it affords to bathopsis in intelligent animals which might be able to get along with only monocular cues to distance, binocular vision has a great advantage over monocular in any animal, as we shall see. But whatever the gain

made by having frontal eyes and wide binocularity, is it likely that animals would seek it if, to get it, they had also to tolerate a perpetual diplopia? It is far more likely that the vertebrates would long since have discarded one eye and come to have a single, frontal, cyclopean visual organ like that of the ascidian tadpole. That they have not done so is evidence in itself that they have always seen singly in the binocular field, that the 'physiologically cyclopean eye' which the psychologists like to talk about, when they are stressing the singleness and straight-aheadness of human vision, is not a primate (or even mammalian) invention at all.

If each side of our owl's brain projects its image of the mouse into the same part of space, will the owl not see one mouse there? Is not his dual projection to the same place, which could be occupied by only one thing, what we mean by fusion? Well, no, not quite; for there might be only superposition of the two mental images of the mouse. This would not be fusion—it would be more like the mess one would have if one projected onto a screen, superimposed on each other, the right- and left-eyed images from an ordinary stereoscopic viewing-card. Would the vision of a total-decussation vertebrate have to be like *that* throughout his binocular field? If it must, one wonders again why the animals with two eyes have not thrown one away or at least religiously kept their two monocular fields from overlapping.

In ourselves, fusion is not through superposition or even a complete blending of the whole of one image with the whole of the other. Rather, it is a sort of mosaic process which is dynamic, with constant shiftings of the conspicuousness of the parts of the images, little suppressions of one part of one or the other as the gaze wanders over the object. In those of us who have a strongly 'dominant' eye, the solid image is mostly the dominant-eye image, with the image of the other eye used to paint in the solidity, so to say. If binocular vision in the lower vertebrates yielded a singleness whose basis was superposition rather than mosaic unification, then their perception of the form and pattern of solid objects ought to be far better with one eye than with two, for the superposition of disparate images would be tantamount to diplopia. But blennies, and chameleons, and birds with temporal foveæ, and mammals all look at things binocularly from choice, even though, if they wanted to, they could look monocularly just as lizards are forced to do by their adherence to a centrally-positioned fovea. Yet, none of these animals is ever observed to close one eye in order to get a better look!

On logical grounds alone, we can thus make out a strong case for believing that the lower vertebrates have singleness of perception of objects in their binocular fields, despite their independent eye movements, and their lack of any system of corresponding points, and their total decussation. The mammals, though ranking higher, seem at first glance to have lost, not gained, something. They are unique in having in combination just these things that the other vertebrates lack—conjugate eye movements, dependence for fusibility upon corresponding points, and partial decussation. We shall see that this combination of mammalian peculiarities expresses a relationship of cause and effect, and that it does represent a gain of something after all.

It is not known whether lower vertebrates can make binocular color mixtures (see pp. 90-1), though if they can do so it would require us to believe in fusion for them. And, the matter should be susceptible of experimental attack. A fish might be trained positive to purple and negative to red and also to blue. Provided then with a red covering over one eye and a blue one over the other, and placed in white surroundings, he might or might not give a positive 'purple' response; and if he did do so, it would indicate fusion. But apart from strictly visual phenomena, there are many indications that the two eyes are interconnected through the nervous system even where total decussation of the optic nerves obtains:

In some fishes at least, one eye can control the dermal color changes of the whole body as well as the two eyes normally do (p. 532). In the rays, there is a consensual pupil reflex—both pupils contract when only one eye is illuminated. In the pigeon, recent work has shown that there is not only a consensual pupil reflex but that usually the two eyes blink when one cornea is touched; and the two nictitating membranes also act consensually. Moreover, in all vertebrates the two eyes are coördinated in their reflex movements, though of course this association of the eyes is strictly motor and has in it nothing of the photosensory element which exists in the control of the pupils and of the dermal chromatophores.

All in all, there is considerable reason to believe that the binocular vision of all vertebrates is *single* vision. The 'independence' of the eyes due to total decussation has been much over-rated. There *is* such an independence, on the motor side; but this does not make it inevitable that there shall be sensory independence as well. After all, our two hands move independently, but when they both grasp the same object its singleness is appreciated without benefit of any partial decussation of the spinal sensory tracts. In the tactual modality of sensation, there is even an

analogy for corresponding retinal points, for if two adjacent fingers be crossed out of sight and a pencil rested between their tips, *two* pencils will be felt in the well-known 'Aristotle's illusion'. Singleness, in the realm of touch, is obviously entirely psychological in basis. In vision, it is equally so—and would never have been thought to be otherwise if the partial decussation had never been discovered by anatomists.

If the total-decussators do have fusion, then as we have seen above there is no reason to deny them binocular stereopsis. If there is singleness created from right- and left-eyed images, stereopsis comes along with it as a sort of psychological windfall.

The Evolution of Binocular Vision—The need for something cannot operate as a cause of it; but we do have a right to ask ourselves just why binocular vision has ever evolved in the first place. What does it give the animal? Clearly, its adoption and extension involves a loss of periscopy and must offer some compensations which outweigh that sacrifice. In ourselves, the chief advantage of binocularity appears to be a precision of object-localization. It does not matter that we see solidly, so long as we see deeply and can say with assurance that one particular billiard ball is two and one-half inches farther away than another. We have this ability only because our two one-eyed images are projected to a common meeting place in space; but independent convergences of our two eyes would still give us parallax on an object, enabling us to locate it more promptly and accurately than we can do with a succession of monocular parallaxes, even if we did not perceive solidity.

We may be sure that animals have not evolved binocularity in order to see solidly. As we have seen, the percept of solidity came to them as an incidental accompaniment of disparate-image-fusion. But they nevertheless have had a powerful incentive to develop binocularity wherever their snouts and their beaks and their requirements of periscopy would permit. This incentive was the fact that the binocular parallactic cue to distance makes no demand upon intelligence. It is as automatic as geometry. On the other hand, for the successful employment of the monocular cues (pp. 313-4), *learning* to use them is a prerequisite:

A human child must learn slowly to evaluate the size of his retinal images. To him, a monster airplane a mile in the air seems like a bird a few yards overhead. He has to be told why the railroad tracks seem to come together, must learn the meaning of shadows. He slowly learns to evaluate aërial perspective, and may be painfully deceived by it when he

starts to hike to a mountain which looks two miles away and is nearer twenty.

But long before it has had time to learn any of these lessons, an infant, not yet able to speak, can employ binocular parallax to reach accurately for a toy. A chick reacts correctly to distance as soon as it is hatched. Considering their greatly inferior mental equipment, were not the lower animals fortunate to hit upon a cue to distance which required no learning for its successful employment, but merely a reflex coördination of the muscles of locomotion with the muscles of the eyes?

Of course, in many animals which give every evidence of depending upon binocularity, the eyes are so close together that they cannot possibly have much parallactic 'leverage'—the angle between the lines of sight, at any great distance, is so small that the binocular cue to distance seems of low value as compared with our own. And, their two views of an object at any great distance are so nearly alike that their stereopsis can only be relatively weak. But—an intelligent lion, looking at our (to his mind) small heads and ridiculously small interpupillary distance, might say the same unkind things about the usefulness of our binocular vision. After all, a small animal may have descended from a larger one, retaining the same facial conformation. A half-pint galago has the same frontality as a dreadnought gorilla, but only a fraction of the gorilla's interpupillary distance. Neither of these species represents the size of the extinct primate which originated primate frontality. Then too, small animals feed on small objects; and, their absolute speed being low, only small distances mean much to them from moment to moment of their existence. Within these small distances, the angle between the lines of sight of their close-set eyes may be just as great as the one between our own visual axes when we look yards ahead at an object in our own path. And it is this angle, not the linear interpupillary distance,* which really counts.

We can set up a rather complex series of 'ifs', as follows:

(a) If vertebrates have sacrificed the ancient periscopy to evolve binocularity, it must be because it offers advantages; but

(b) If they have binocular vision of an object, they would gain absolutely nothing from binocularity if they saw the object diplopically; so

*The interpupillary distances of some of the larger animals may be of interest here. Years ago, Berlin published the following figures (among others): young African elephant, 49 cm.; horse (average of 20), 19.6 cm.; cow, 18 cm.; axis deer, 14 cm.; llama, 12 cm.; chamois, 10 cm.; goat, 9 cm.; sheep, 8 cm.; man, 6 cm.

(c) If they see the object singly with two separate eyes, they must have fusion of the two images of the object. Now:

(d) If they have fusion, they have parallactic localization of the object in space; and

(e) If they have fusion of their disparate right- and left-eyed views of a solid object, they have a percept of its solidity.

But if all these ifs are true, they still leave unexplained why the optic nerves became incompletely decussated in the mammals. If our reasoning so far is correct, partial decussation is no prerequisite at all for fusion and stereopsis. What, then, does depend upon it, and what special ability has it given to the mammals which lower forms do not possess?

It has already been pointed out that partial decussation is associated with conjugate eye movements and with corresponding retinal points or fixed local signs of direction. If a fish with unconjugated eye movements can look at an object now with the eyes in one position, now in another, there are surely no fixed local signs of direction in the retina of the fish, and no corresponding points. And, if a dog can see a rabbit singly with one degree of convergence at first, and with another degree when he has become excited by the chase, there would seem to be no corresponding points involved. But where the eyes have become completely conjugated in their movements, so that looking to a certain distance always means a particular degree of convergence, then fixed local signs of direction, or correspondency of points, could logically be evolved and could never be detrimental so long as the conjugation remained perfect.

When conjugated eye movements were evolved by the mammals, this led to the freezing of local directional signs, which then ceased to depend upon the position of the eye in the orbit. This in turn made the mammals dependent upon the system of corresponding points for the maintenance of fusion. How, then, did the conjugation itself arise? Well, if we wanted to revise the nervous system of a fish or a bird to facilitate conjugation of the eye movements, we could not do better than to connect each retina to each of the nerve centers which in turn are connected with the muscles of both eyes. Then, community of vision of the two eyes could be most conveniently made to result in community of action. With the two eyes seeing the same thing, it is optically desirable that they each face it squarely. If, when one eye aims at and accommodates for a particular point in space, the other eye automatically aims at and accommodates for that same point (even if covered, or even after the eye-muscles have

been surgically scrambled—pp. 311-2) we then have a situation superior to that in, say, the chameleon, each of whose eyes has to locate the prey insect by itself before the cerebral navigator can work out the position of the insect by a process of triangulation.

Partial decussation of the optic nerves accomplishes just this desirable tying-up of both retinæ to both the left-brain and the right-brain centers of eye-muscle control. In the thalamus, not far from the groups of nuclei which operate the eye muscles, there are way-stations on the sensory pathway from the retina to the cerebral cortex. These way-stations, the lateral geniculate bodies, are connected by way of the superior colliculi with the nuclei of the eye-muscle nerves. Here, then, is the real terminus of the optic nerve fibers so far as concerns any importance of the fact that they come into each side of the thalamus from both retinæ instead of from only one. The fact that in the higher vertebrates *bi*-retinal impulses continue on up to each half of the cerebral cortex then becomes altogether meaningless; for in whatever patchwork fashion the two optical images finally arrive at the cortex, the two (left and right) cortical image-patterns are due to be fused into one pattern anyway. The whole aim and goal of partial decussation has already been attained down in the thalamus and the tegmentum, where what *one* eye is seeing is enabled to control the motor impulses to *both* sets of eye muscles.

Partial decussation is thus explained, not as the indispensable basis of binocular single vision, but as a logical eventual consequence of binocularity. Its value is not in the immediate field of conscious sensory phenomena at all, but in the realm of motor activity where it serves to facilitate the motor coöperation of the two eyes. Partial decussation has never arisen in the owls or the frontal-eyed deep-sea fishes, perhaps not because (or not only because) these are not mammals, but because their eyes are motionless.

The evolution of their motor conjugation has made the mammals completely dependent upon it for singleness of binocular vision and for accurate space-perception, for along with it there arose the phenomenon of corresponding points. This dependence is at once spot-lighted when anything goes wrong with an eye muscle or its nerve, and a strabismus or squint develops—one eye turning out or in so far that diplopia occurs. We can perhaps best understand the relation of corresponding points to eye-movement conjugation, and understand how the lower vertebrates get along without both, if we consider the phenomenon of the substitute macula.

Invariably in a strabismus patient the fovea of the inturned eye loses its directional sign; but occasionally a patch of the nasal retinal periphery, which is now aimed into space along a line parallel to the other eye's visual axis, takes on the quality of a corresponding spot paired with the fovea of the good eye. The previous diplopia slowly fades away and the patient becomes capable of fusing the image on the fovea of the normal eye with that on the 'substitute fovea' of the squinting eye. If now the squinting eye is straightened by an operation, its fovea will regain its old community of direction with the fovea of the other eye, and temporarily there will be a *monocular diplopia* in the operated eye—until the latter's substitute macula has had time to 'fade' and regain its original notion of direction.

These processes, under favorable conditions, may require weeks or months. We can describe the essentials of what has happened, by saying that a spot on the retina of the squinting eye has taken on a new local sign of direction because the eye has taken a new position in the head, with the result that the same objects, in the same places in space, are now *seen* in those same places, as before. When we have said all this, we have really also described what happens in the lower vertebrates with total decussation, when they perform their independent eye movements. The only difference is that the alteration of local directional signs is continuous and instantaneous as the animal turns the eyes about, while in man the local signs are so firmly fastened to particular retinal points that changing them is an extremely slow process and is seldom possible at all! The mammals indeed lost something when they developed the partial chiasma for the sake of conjugating their eye movements.

In conclusion, then: the vertebrates which have much of a binocular field have always had singleness of objects in that field, and perceive them as 'solidly' as their inter-pupillary distances allow. The need of a permanent coördination of eye movements for rapid and precise estimation of distance was finally met in the mammals by the device of partial decussation in the optic chiasma, putting the oculomotor apparatus in control of the pair of images and making it responsible for the maintenance of fusion. Conjugation being attained, a system of fixed local retinal signs of direction could now develop, with a consequent improvement of the precision of localization through the appearance of a new cue to distance—the physiological diplopia (and haziness) of objects which are off the horopter, and which only disappears when convergence and accommodation have hit their mark precisely. But, the animal now

being utterly dependent upon the stimulation of corresponding points for his singleness of vision, his perception of space and his visual comfort are at the mercy of any slightest pathological or traumatic disturbance of the neuromuscular tie-rod which, at his bidding, turns his team of eyes.

The Nature and Basis of Fusion—By this time, the reader may have in his mind a rather confused idea as to what 'fusion' actually is. Where the separate monocular images are perfectly identical, as when two prints from the same negative are placed in a stereoscope, the binocular fusion-image differs in no way from the monocular image on either side. The fusion-image could be adequately represented by projecting on a screen, superimposed on each other, the two pictures on such a stereoscope card. But this is a special case—ordinarily, the objects at which we look binocularly have depth or thickness, and our two monocular images of them are not identical. We have noted above that the pattern of the everyday binocular fusion-image is *not* such that it could be represented by mere superposition of the monocular images. We can perhaps imagine that in some way the whole of a right-eye image is integrated with the whole of a slightly-differing left-eye image, without this resulting in an effect like that of superposition. But *is* the fusion-image, whether tridimensional or flat, of this all-of-right-plus-all-of-left character?

If it really were, then we should expect to find in binocular vision two phenomena which it does not in fact exhibit: (*a*) binocular visual acuity should be greater than monocular*; (*b*) binocular brightness should be greater than monocular. Neither of these things is true of human vision in general, though there does seem to be some summation of the monocular brightnesses in intensities close to the rod threshold. If binocularity in itself conferred higher visual acuity, or increased the overall sensitivity of the visual mechanism to light, then these great advantages would alone be enough to account for the repeated evolution of binocularity by both diurnal and nocturnal vertebrates of all sorts. The parallel visual axes of such forms as the owls, galagos, and deep-sea fishes have indeed been very often explained on the assumption that the binocular-vision phenomena of such animals include a summation of the two monocular brightnesses. And we have seen reason to suspect that binocular acuity

*Binocular visual acuity in this sense, which is the resolving power of the two eyes together as compared with that of one eye alone, is not to be confused with the more common term 'stereoscopic visual acuity'. This latter term refers to the accuracy of binocular distance- or depth-perception.

may be 'summated' in some vertebrates even though it is not in ourselves (see p. 308).

It seems odd that binocular resolving power should *not* be always higher than monocular. When we consider that the receptor mosaic of one retina, like a halftone reproduction, can register only certain of the points on an object's surface, then obviously the chances are preponderant that at any one moment the other retina will be recording a set of points which fall mostly in between those of the first set—just as one retina 'fills in' the blind spot produced by the head of the optic nerve in the other retina. If now the two sets of object points are interdigitated in a fusion-image, why is not that image as well resolved as would be the monocular image supplied by a retina containing nearly twice as many receptors per unit area as either member of the pair of retinæ we are

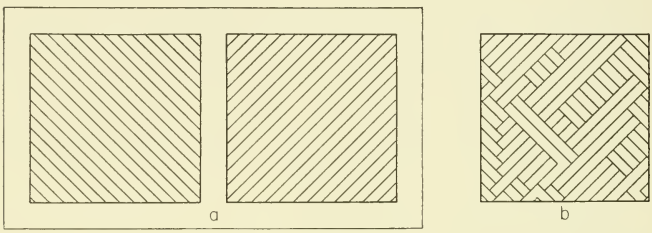

Fig. 122—Retinal rivalry for patterns.

a, stereoscope card bearing unlike patterns. b, the sort of mosaic which one may see, at any one instant, while observing a in a stereoscope.

considering? One would expect this, just as one expects to gain a better idea of the form and texture of an object by holding it in two hands instead of in only one. The bothersome fact remains that when the two eyes are in use our resolution of details is just as good as, and no better than, the resolution afforded by the better of the two eyes when that eye alone is used.

This calls for explanation. We can offer a weaselly sort of teleological reason why binocular brightness should not be raised over monocular—at least in diurnal animals, such as man: if binocular brightness were allowed to be higher than monocular, contours would be created between the binocular and uniocular visual fields, and these might be as perpetually disturbing as those seen by a person who cannot get used to

his bifocal spectacles. But there seems no reason for the evolution of a special central mechanism for inhibiting any enhancement of visual acuity that might accrue from the integration of the two monocular images.

That integration must, then, be of a sort which somehow makes impossible any real interdigitation of two complete monocular sets of image points in a therefore-twice-as-well-resolved binocular image. This condition will be satisfied if the fusion image somehow partakes of the nature of a gross *mosaic*. And that it does do so, at least where fusion of patterns is concerned, is suggested by the phenomenon of 'retinal rivalry':

Suppose we observe in a stereoscope (Fig. 117, p. 316) a card, the two pictures on which are like those in Figure 122a. We might reasonably suppose that the two sets of diagonal lines would be fused into a perfect grid; but they are not—what we see is a mosaic, composed from the two sets of lines, which constantly shifts but which, at some one instant, might look like Figure 122b. At no time do we see a standing grid pattern, either throughout the whole square or even in some small area thereof. Instead, the two unlike patterns vie for a place in consciousness, and at any one time *parts* of *each* pattern are *wholly* successful.

The image in such situations is generally deemed the very apotheosis of a *non*-fusion image. But there has long been a theory, favored by a minority of psychologists, that the everyday binocular image partakes of the same ever-changing mosaic character as the rivalry image. It only fails to exhibit rivalry (and hence fails to reveal its mosaic character) because the two images being dovetailed together are identical or (where the object is tridimensional) only slightly unlike—never as greatly different as are the two patterns of Figure 122a. Intra- and interhemispheric fusions are thus essentially the same, for both involve putting left- and right-eyed fragments side by side in the total image (Fig. 121a, p. 321).

This mosaic theory of fusion has not yet had an adequate experimental test, but it holds considerable promise. However, though it accounts beautifully for the equality of binocular and monocular acuity and brightness, it is helpless to explain the binocular mixture of colors. One can obtain rivalry between, say, red and green monocular areas in a stereoscope. But under proper conditions the red and green fuse into homogeneous orange, which is not of heightened brightness, and yet has no appearance of being a mosaic of red and green. It would seem that the single images resulting from the binocular fusion of complementaries, or of other miscible colors, must of necessity represent the fusion of *all* of the right-eye image with *all* of the left-eye one.

The fusion of pattern and the fusion of color thus seem to be two very different kinds of fusion. But though both pattern vision and color vision are equally attributes of the retinal cones, there is room for believing that they reside in different parts of the central nervous system (see also pp. 521-3). On each side of the brain there may be two distinct fusion centers, one being for pattern and the other for color. In such centers, should we find them anatomically, we should have a basis for a perhaps entirely physiological fusion of impulses stemming from both retinæ. The basis of the psychic act of fusion (see p. 322) of the two fusion-images (one in each side of the brain) into one cyclopean image—and the basis of this, the only kind of fusion present in species with binocular fields but with totally-decussated optic nerves—would be still to be sought, presumably in an inter-hemispheric interchange of information through commissures.

There is, indeed, good neurological evidence for the existence of two binocular fusion-loci in each half of the mammalian brain. One of these may be the residence of pattern fusion, the other of color fusion, and we can even hazard a shrewd guess as to which is which. In the past two or three decades many neuro-anatomists and neuro-physiologists have come to agree that the right- and left-eye pathways, which are separate in each optic tract, maintain their separateness past the synaptic center in the lateral geniculate nucleus, all the way to the visual cortex in the area striata of the occipital lobe. Here, 'layer IV' of the general sensory cortex—the layer in which awareness in general resides—is triply laminated in primates, and locally presents so-called supragennari (IVa), mesogennari (IVb), and infragennari (IVc) sub-layers (Fig. 123).

Studies of the brains of traumatic and experimental one-eyed individuals, in man and other species, have shown that the infragennari lamina receives only fibers which, coming from the lateral geniculate body of the same side of the brain, are there connected with optic-tract fibers hailing from the retina on the other side of the head. Total decussation being the primitive situation, the infragennari layer is likewise primitive, and its physiological counterpart could presumably be identified in any vertebrate which has a visual cortex at all. But the supragennari layer, or its equivalent in non-primates, receives only fibers connected with *uncrossed* optic-tract fibers. This layer is lacking in the cortical areas upon which the uniocular fields are projected, and is of course greatly reduced in species whose binocular visual fields are narrow.

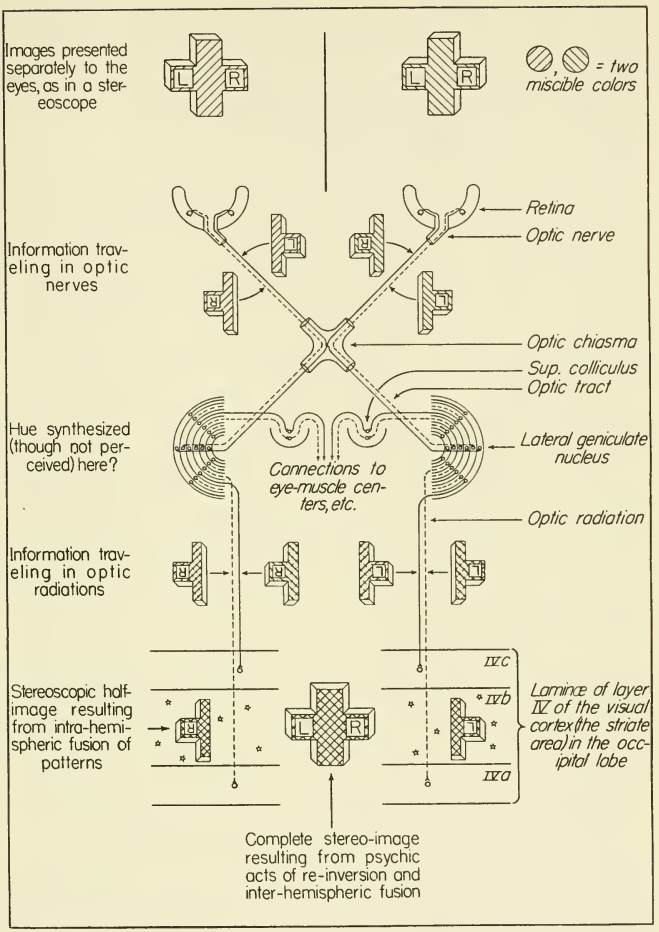

Fig. 123—Afferent visual pathways and events in binocular vision, in primates. (In most other mammals the laminations of the lateral geniculate and of layer IV are less clear-cut).

The mesogennari layer is unique in the presence there of numerous 'star' cells. It is not disturbed, but both the infra- and supragennari layers are subject to atrophy, if the receptors connected with them are removed. Thus for example, in the brain of a man who has lived for some time minus his left eye, the left supragennari and the right infragennari laminæ of layer IV will be found to be atrophied.

The implication of the sandwich-like morphology of layer IV is that the mesogennari layer is the locus not only of some or all of visual consciousness, but also of the fusion of ipsilateral and contralateral information sent by the two retinæ to the top and bottom layers of the sandwich. The mesogennari layers of the two sides of the brain thus constitute, taken together, the 'binocular center' which earlier (pp. 90-1) we saw to be always employed even when one eye is used alone. Again, both mesogennari layers are involved even in 'hemianopic' vision. Each of them represents one half of the whole visual field (consult Fig. 123). Now, if the right or the left optic tract is severed by injury or disease, the individual is thereafter blind in respectively the left or the right half of his erstwhile visual field. Even so, he can experience contrast effects between his seeing and his blind fields. Thus, if he looks at a bright surface long enough to develop an after-image, he will have a bright after-image in the blind half. Similarly, if he looks at a colored surface he 'sees' the complementary color in his blind field, and in turn the complementaries of both of these colors in the two halves of a chromatic after-image. Only an interaction of the two sides of the cortex could account for such phenomena.

A fusion of left- and right-eyed information thus occurs in each mesogennari layer, and between the two mesogennari layers an interhemispheric fusion takes place, creating the cyclopean image—whether this be flat or stereoscopic. Presumably, if a symmetrical lesion should destroy either both infragennari layers, or both supragennari laminæ, the individual would retain a complete visual field (so long as both eyes were open), but would no longer see stereoptically. No clear-cut case of this sort has yet appeared in the neuropathological literature.

In man, layer IV appears to be the locus of the entirety of visual awareness. At least, if the areæ striatæ, or the whole occipital lobes, are destroyed, the result is total blindness. Something of vision might remain, of course, if only layer IV were selectively destroyed—we do not know, since this never happens accidentally and would be impossible to accomplish experimentally. In lower animals, certainly, some aspects

of vision persist even after the loss of the whole of both occipital lobes. Rats, and even monkeys, can make discriminations of differences in intensity after bilateral occipital lobectomy. Removal of one lobe should theoretically produce no change except to create hemianopia—vision in only half of the field—but it has been claimed that in the chimpanzee there is a slight but permanent impairment of visual acuity following unilateral occipital lobectomy. In man, mild lesions of one or both areæ striatæ alter or destroy color vision in half or all of the visual field, but achromatic sensations remain intact unless the lesion is more serious—the sense of brightness being particularly durable. Here again, we have evidence that hue is recorded centrally by a mechanism distinct from that mediating the remainder of vision.

As regards intra-hemispheric binocular fusion, it might seem that both color-fusion and pattern-fusion would have to occur in the mesogennari lamina. *Consciousness* of the products of the fusion-processes assuredly occurs only there, in man. But it is quite possible that some visual information from the two eyes is mixed together below the brain-level at which it gets into consciousness. In the highest vertebrates, the lateral geniculate nucleus affords a one and only opportunity for such pre-conscious mixture:

The lateral geniculate (Fig. 123) is the only way-station on the pathway of visual sensory impulses from retina to cortex. In the optic nerves, the fibers are in fascicles, each representing a spot of retina; but in going through the chiasma these bundles fray out. By the time the crossed and uncrossed fibers enter the lateral geniculate body, they are so intermingled that just about every crossed fiber has an uncrossed one running alongside it. Within the lateral geniculate, the synapses with geniculocortical fibers are intimately intermingled in an elaborate lamination which gives the geniculate a rather more complex structure than even the cortex itself. This multiple lamination of crossed and uncrossed synapses implies that some aspect or aspects of binocularity are handled in the geniculate, as otherwise the interweaving, there, of the right- and left-eyed optic pathways seems meaningless in view of the fact that they must later be untangled again in order to enter the laminæ of layer IV independently.

It appears, then, that the synthesis of monocularly or binocularly mixed colors may very well be accomplished in the geniculate, so that although there is no awareness of the color until the cortex is attained, the information carried through the optic radiations already has the

colors mixed. The (mosaic?) fusion of brightness-patterns in the mesogennari layers follows, and the total picture of visual space is synthesized through the inter-mesogennari connections in the corpus callosum.

Speaking against this view is the fact that color vision is so much more readily disturbed than brightness vision, by cortical lesions. The anatomical facts will fit, as well, an alternative hypothesis that it is *pattern* which is fused in the geniculate, *color* in the mesogennari layer. In rats and monkeys, consciousness of the brightness patterns, whether already fused there or not, resides in the lateral geniculate. And, the cat, which has no color vision, has almost as complex a geniculate as man—and therefore, in the cat (and hence in man?) its structure cannot be purposed to accomplish color mixture.* In any case, upon the culmination, in man, of a completely equal representation of the two eyes in each side of the brain, consciousness seems to have been made to wait upon intra-hemispheric fusion, and both processes have been pushed up into the cortex insofar as achromatic sensations are concerned. In animals which have totally decussated optic nerves, and hence have no intra-hemispheric fusion to be accomplished, the whole of visual consciousness is enabled to sit at a relatively low level (ordinarily the optic tectum—see p. 522) of the central nervous system.

The Strange Fate of the Median Eyes—One of the conclusions reached above (that the vertebrates have always had single vision in the binocular fields of their lateral eyes, whatever the structure of the optic chiasma) may shed some light on the curious history of the median eyes:

There are indications, from elasmobranch embryology, that the protovertebrates possessed a metameric series of paired visual organs on the roof of the head. Most of them rapidly disappeared as the lateral, ordinary eyes became perfected; but two pairs of dorsal eyes still hung on almost until the cyclostome level of evolution was reached.

In most modern cyclostomes, two dorsal eyes are present (Fig. 124). They do not represent a pair, however, for they are arranged in tandem with one behind and below the other. Neither is squarely on the mid-line of the head—instead, one appears to join the roof of the diencephalon to one side, the other on the other side, of the sagittal plane. These two

*Le Gros Clark has recently suggested that the six layers of the primate lateral geniculate (three connected with one retina, three with the other) are related to the three fundamental hue-sensations described by the Young-Helmholtz theory (see pp. 91-6). This is hardly possible, since cats, phalangers, and other nocturnal, achromatic mammals also have laminated geniculates—sometimes even with *odd* numbers of layers.

sub-median eyes of the lamprey, the 'pineal' and 'parietal', thus seem each to represent one member of an original pair (Fig. 54, p. 126). In the same way, the one eye of the ascidian tadpole (see p. 121) is situated off the mid-line and seems to have a mate in the form of a vestigial mass of tissue on the other side of the head (Fig. 48d, p. 122).

Neither of the median eyes of a lamprey is built well enough to have images, or anything more than the ability to record the intensity and perhaps the direction of light. In vertebrates higher than the lampreys,

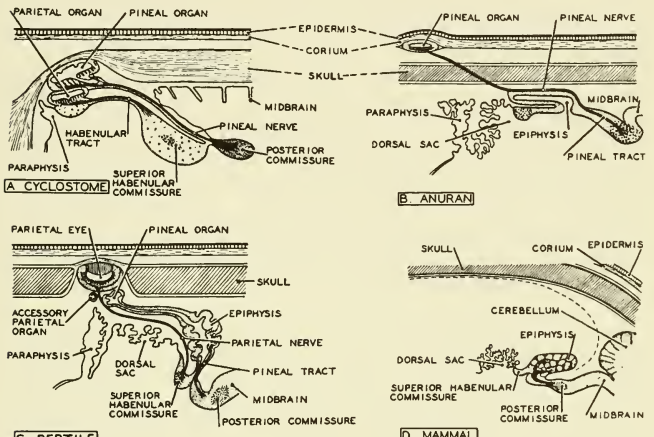

Fig. 124—Condition of the pineal and parietal (parapineal) eyes in various vertebrates. After Neal and Rand.

only one of these eyes is ever to be found. The stegocephalians must have had the pineal eye at the height of its development (Fig. 61b, *p*, p. 137), if we can judge from the size of the foramen for its nerve in the stegocephalian skull. But in modern amphibians it is vestigial, in the frog a mere cyst underlying the skin of the 'brow spot'. In birds it has gone completely, and in mammals it has been converted into the 'pineal gland' of dubious, possibly endocrine, function.

The parietal eye must have been somehow represented in the stegocephalians; for, though it is completely lacking in modern fishes and amphibians, it is present as the sole median eye in modern reptiles. It is

functional and provided with a lens and a fairly fine-grained retina in *Sphenodon* and in some lizards.

One can understand why the eventual single parietal eye of the reptiles should have ceased to be an eye, and disappeared, in their avian and mammalian descendants; for, being unprovided with lids, it could not clear a way for its operation through the shrubbery of feathers or hair. But a good question which has never been answered—perhaps never even raised before—is: why did the median eyes ever lose their bilateral paired condition, and why was one member of the lamprey's tandem combination eliminated by higher forms which perfected the eyes but kept only one of them?

This question is not of any real importance; but it is an interesting one, and perhaps we can answer it in the light of the foregoing discussion of the universal fusibility of the binocular images of the lateral eyes. It seems quite possible that the dorsal eyes, being less fortunate in their connections within the brain, yielded sensory impressions which were incapable of any sort of fusion—just as our two hands, separately and simultaneously touching steel and leather, give us normal impressions of those two materials and not of a single hybrid substance of intermediate or summated properties.

If no fusion could be accomplished between the members of a pair of dorsal eyes, no harm was done as long as the eyes were not capable of seeing *pictures*. But as their lenses evolved and their retinæ improved, this point of perfection was reached and difficulties arose. So far as we can tell, none of these median eyes ever had any muscles to move them, or indeed any accessory organs of any kind. With rivalry or diplopia occurring in each pair, the number of pairs was radically reduced to two, and one member of each pair was discarded (Fig. 54b and c, p. 126). When at last the eyes became such good ones that diplopia between the unconvergible tandem eyes became intolerable, one of them had to go. The solitary remaining median eye could then be perfected to any degree by the ancient amphibians and early reptiles, without further diplopic trouble or even any danger of its field of view overlapping into the fields of the lateral eyes.

The reptilian lateral eyes are such very fine visual organs, however, that in this group the median eye lost most of its importance. Gone in the turtles, gone in many lizards and in all snakes, it was already well on its way out of the vertebrate picture even before it was finally buried beneath the plumage and fur of the birds and mammals.

Substitutes for Binocular Stereopsis—It would be rather hard to say which of the possible monocular cues to distance (pp. 313-4) a given animal can and does use. But one of these cues, the production of parallax by head movements, is also valuable for throwing objects into 'relief'; and when an animal habitually employs this process the fact is quite evident. A number of lateral-eyed vertebrates, whose binocular fields are so narrow as to be practically useless, obtain a perception of solidity and relief—a sort of monocular stereopsis—by invoking parallax in one way or another.

When, as children, we dropped a prized penny upon a brown rug on which it became invisible, we located it by getting down on the rug and placing an eye close to its surface, so as to see the profile of the coin in relief. A few years ago, Joseph Grinnell called attention to the fact that there are many birds which do something quite comparable. Birds either eat moving food, pursuing it or waiting for it to come along; or they seek motionless food, such as seeds. Birds in this latter category perform what Grinnell called 'rapid peering': they cock the head this way and that several times before pecking at a seed or berry, thus placing it in relief against its background from several different angles in quick succession, and identifying and localizing it with precision before pecking it with assurance.

The shadow cast by a solid object gives it relief, for when seen from more than one angle either simultaneously (as in binocular vision) or successively (as with rapid peering), different amounts of the shadow are visible and the prominence of the object can then be evaluated. Benner has recently shown that in the pecking of grains by chicks, the shadow is of great importance. If the kernels were so illuminated that their shadows were eliminated or displaced, the chicks ignored them. Painted representations of shaded kernels deceived them, though Benner says that they seemed aware that they were being fooled. One-eyed chicks were as well able to peck accurately as two-eyed ones, for both used only monocular parallax for ascertaining distances. Apart from experiments, we have abundant evidence of the importance of shade and shadow to animals for their perception of relief, in the form of the many dermal camouflaging devices adopted (particularly by insects, fishes, and reptiles) for obliterating shadows or for creating 'false relief' through the use of color spots graded in tone. The interested reader should consult the work of Cott listed in the bibliography.

Some birds when walking (fowls, pigeons, doves) and others when swimming (coots and gallinules) make perpetual forward-and-backward oscillatory movements of the head. It has been claimed that the eyes never actually move backward through space—the forward movement of the body just cancels the backward movements of the head. Thus although the body moves forward steadily, the head moves forward through space by jerks and pauses. In effect, the eyes obtain a rapid succession of previews of the surroundings from constantly new angles. The forward movements of the head being so quick, each new parallactic observation of the field is made almost simultaneously with the preceding one, and the exaggeration of the apparent relative motions of objects at different distances furnishes a basis for the estimation of distance and relief.

Many shore birds bob their heads vertically as they teeter along the beach, and many snakes weave their heads from side to side during scrutiny. Some birds and many lizards commonly have spells of nodding periodically. These habits have been interpreted as devices for producing an artificial relative motion in the surroundings. Many herpetologists believe that the nodding of lizards is a sociological phenomenon —the animals do it most when they are among their fellows, when they are warmed up, well-fed, when they 'feel good' and so on. But this only means that they nod most when they are in normal condition and on the alert. The habit does not seem to be sexual; and if it is social at all it is still not without visual importance. If a lizard nods mostly in the presence of other lizards, that may merely signify that for a lizard nothing so much merits close scrutiny and visual cogitation as does another lizard.

(E) Movement-Perception

Human vision is such an enormously rich complex of experiences, and human beings are so diversified in habits and interests, that no two of us value our eyes for quite the same set of reasons. If asked what aspect of vision means most to them, a watchmaker may answer "acuity", a night flier, "sensitivity", and an artist, "color." But to the animals which invented the vertebrate eye, and hold the patents on most of the features of the human model, the visual registration of *movement* was of the greatest importance.

Any sense organ exists not simply to give its owner awareness of some physical, environmental agency, but to provide a basis for awareness of

change in the force or the substance which it records. The most important changes in visual stimuli are changes in their locations. No sense other than vision is at all reliable for the orientation of animals with respect to the objects in space—bats, with their miraculous ears, again excepted. And, the big reason why it is vital to know where things are is that some of those things, and the animal itself, move. Indeed, if nothing on earth moved, there would never have been such things as eyes. Plants do not have them, and neither do sessile relatives of eyed animals—sea-lilies and barnacles, for example.

But all vertebrates move about, even if a few, like the ectoparasitic dwarf males of certain fishes, do not do so under their own steam. Always, the vertebrate eye has recorded movement, regardless of the evolutionary ups and downs of its capacities for sensitivity, acuity, and color-reception. We can imagine vision with any of these aspects close to the vanishing point, but not vision without awareness of motion. Psychologists are fond of pointing out that a wiggling finger, seen in the extreme periphery of the visual field, is not seen as a finger with a certain brightness, color, and form, but is perceived as pure, disembodied wiggle. Vision in the periphery being crude and 'primitive', the conclusion is often drawn that *motion* is just about the most ancient and primitive aspect of vision. Motion may persist when all else is lost—an individual with a large scotoma or with hemianopia (*v.s.*) may see the motion of objects (though not the objects) in what is otherwise a completely blind field.

Detection versus Saliency—If the biological need for a capacity to perceive movement varies from animal to animal—and it obviously does—we may reasonably look for differences in this capacity. But although we may be able to see morphological and physiological differences which should affect the movement-seeing capacity, we cannot very well assay another set of factors which is of enormous importance. These are the psychic factors which have to do with the conspicuousness in consciousness, the *saliency,* of movements—with their 'attention-value' and importance to the animal, in other words. Animal *A* may have a far poorer objective basis for detecting movements than species *B*; yet we may find that species *A* gives a violent reaction of fear or flight to a slight motion in its surroundings, while animal *B* calmly contemplates moving objects without making any overt response to them. Here, we can attempt to evaluate only the most nearly objective factors in movement-perception. The subjective factors which endow motion-percepts with their

greater or lesser saliency must go largely undiscussed since we know so very little about them in man, and still less about them in the other animals.

Naturally, there is a rough correlation of saliency with feeding habits. The well-armed carnivore does not need to be so fearful of unidentified moving objects as does a timid and defenseless herbivore. For, in wild nature, a moving object is generally another animal, and the observer's responsiveness to it will depend upon the importance, to him, of reacting in a motor way to another animal's approach.

Movement may thus have unequal attention value and exciting power for animals whose apparent objective basis for detecting movements is about the same. Or, animals with vastly different eyes may respond to moving and motionless objects in very similar ways. For instance, a frog will snap only at small moving objects—which, in his natural surroundings, are ordinarily things which are good food for him. A penguin will seize and eat only living, moving fishes. Though the penguin's visual capacities (including those which we think have a bearing upon the detectibility of movements) are vastly different from the frog's, either animal could be perched on a mound of its natural food, fresh-killed, and would proceed to sit there and starve to death. Such is the power of moving matter over animal minds.

In general, the less well developed the area centralis or fovea, the more dependent is the animal upon the movements of objects for their detection and evaluation. The penguin is probably an exception—he sees a motionless fish well enough, but instinct tells him that a dead (*i.e.*, motionless) fish is not good to eat; and his olfaction, as in all birds, is too poor to differentiate fresh-killed fish from stinking carrion. Lacking sharp vision, an animal not only misses many sidewise movements, but is readily stalked by an enemy which is careful to approach in a straight line. Recognition of such *toward*-movements depends upon appreciation of the 'growth' of the retinal image—which is poor where acuity is low, both for direct reasons and also because poor accommodation always accompanies poor resolving power.

Not only amphibians, but most snakes, lizards, and many carnivorous turtles appear not to see motionless prey. Motion is particularly important to diurnal snakes, whose visual acuity is probably the lowest of any diurnal vertebrates—*Dryophis* being a conspicuous exception in its ability to secure motionless prey solely by sight. Other diurnal snakes 'lose contact' with the prey if it stops moving or freezes, and then attempt to

regain rapport through olfactory exploring or trial-and-error tonguing. Nocturnal snakes, many of which have superb olfactory powers, are better able to locate and strike motionless prey, without need of vision.

Though all birds have high visual acuity, hawks and insectivorous forms are dependent upon motion for seeing prey at great distances. The bird sitting on a fence-post may fly suddenly and directly to a point rods away, pick up an insect, and return. This is a marvellous ability; but we should not credit the bird with distinguishing a *motionless* bug at such distances. In all probability the bug was moving or the bird would not have seen it; and this is not entirely a matter of the saliency of the movement, for, as will be brought out later, the same object can be distinguished about twice as far away, if it is in motion, as when it is still.

Mammals in general are also quite dependent upon motion. The successful use of the habit of 'freezing' by rodents and ungulates is in itself an evidence that the carnivores which prey on them do not identify them visually when they are still. Two or three breeds of dogs—the borzoi, the greyhound, and to a less extent the dachshund—hunt by sight and must keep the prey in sight or give up the chase; but such a situation is rather artificial for a carnivore and is to be laid to the effects of breeding. Small-eyed, nocturnal mammals are particularly dependent upon the movements of their enemies for apprisal and escape. As we shall see, the eyes of such animals as rats and mice have been called adapted to see motion; but the truth is that they see motion better than form and color only by a process of elimination—they are simply not good enough to see anything *except* the gross movements of large objects.

Grades of Movement—The most obvious basis upon which we might classify movements is their speed. But speed is entirely relative, and is related to the animal's own speed of movement. What may seem very slow to a rabbit, may seem whizzingly fast to a snail. Obviously, the same sensory and perceptual machinery is set in motion whether an object moves past an animal or the animal moves past the object. What occurs is a relative change of position of the two, and the animal's capacity for maintaining a clear impression of an object must be adequate to cover the speeds attained by natural objects important to him, as well as his own locomotor speed among such objects when the latter are motionless. The speed at which it is safe for an animal or a man to travel is largely determined by his reaction time; but it is obviously not safe for an animal to be unable to see an approaching enemy as anything more than a blur,

unless he can easily outrun that enemy. We may be sure that any animal can see, as clearly as if it were motionless, any object moving as fast or somewhat faster than the animal himself can go. It will be recalled that, other things being equal, the size of an animal's eyes is related to his speed of locomotion (Leuckart's ratio). Bearing in mind that visual acuity tends to rise with eye size (see p. 171), we shall shortly see why this should be.

Some objects move too slowly or too fast for any motion to be seen. Suppose we consider only perceptible movements, and separate them into slow, medium, and fast. The ranges of absolute speeds embraced by these terms will vary from species to species and, of course, with the distance of the moving object from the observer. Let us call 'slow' all movements during which the character and details of the object are as clearly seen as when the object is still. There will be even slower movements which will not be seen at all. When we watch the minute-hand of a clock, for example, we are aware from time to time that it has taken a new position; but we cannot honestly say that we see it move. Let us coin a term and say that the movement of the clock hand is for us, psychologically, *infra-perceptible.*

The fastest movements we can detect are those in which we are unable to detect direction. An object can flit so rapidly across the whole visual field that we are unable to say whether it went from right to left or from left to right. Here, we do perceive motion, but not a movement at a certain rate over a certain distance. Still faster objective movements may be *supra-perceptible,* where the speed is so high that nothing is seen at all.

By elimination, 'medium' movements are those in which not only a change of the position of an object can be detected, but also the *changing* of position. The nature of the moving object can be made out more or less well. It is with the perception of medium movements that we are most concerned. The whole percept of such a movement may be described as a comet, whose head is the object and whose tail is a blur which we interpret as 'movingness'. When a cartoonist suggests motion by putting a series of partial outlines behind an object, he has wrought, better than he knows, a realistic diagram of movingness as a train of overlapped after-images.

So, objective movements may be:

A. Infra-perceptible—so slow that only a change of position is noted from time to time.

B. Perceptible as:

1. Slow—where the percept is, so to say, all object and no blur.
2. Medium—where the percept is comet-like, the object being seen with a tail of blur, or 'movingness'.
3. Fast—where the percept is all blur and no object, with direction difficult or impossible to decide.

C. Supra-perceptible—so fast that nothing is seen at all.

All of these definitions, it is understood, concern movements of objects which are not being followed or 'pursued' by the eyes. Where voluntary pursuit eye movements occur, all rules are off with regard to the changes of the appearance of the moving object with changes in its speed. The object may be seen as clearly as if motionless, if the pursuit movements are precise enough to hold its image on the fovea. But even though this image does not move over the retina, the images of background objects do so move, and their apparent speed of movement helps us to gauge the speed of the moving object.

The Relativity of Movement-Perception—Relative movement of the object and its background is essential for any accurate perception of slow motions. In a darkroom, a single spot of light may be motionless and yet appear to be moving, or moving and appear to be motionless; for, eye movements of which we are unaware are then taking place and the shift of the image of the spot over the retina is misinterpreted. This is the explanation of the 'autokinetic movement' of a stationary spot of light which we attempt to fixate, and think we are fixating, but which seems to wander here and there over a considerable range. If two lights are presented and only one is moved, we may see both as moving if they are alike; but if one is larger or brighter than the other it tends to take on the attributes of a 'ground' and we see the *other* light as moving even though it may be the one which is actually stationary. For us to be sure that an object is moving, it is ordinarily necessary that we be able to see some other object which we know or believe to be stationary. In fact the more other, motionless objects we can see, the better for our accuracy in detecting the direction and extent of a motion. The minimal angular velocity for our perception of motion is only one or two minutes of arc per second of time when there are stationary objects in the field; but when there are no such objects to serve as landmarks, the velocity of the moving object must be made ten to twenty times as great. The local signs of direction, and of change of direction, in our retinæ work well

only in a visual field which has *pattern*. The perception of a real movement does not depend solely upon a displacement of an image on the retina, but upon a displacement relative to the images of other objects. Visual orientation in space becomes as imperfect as auditory, as soon as visual space is greatly emptied of reference-objects.

Motor Factors in Movement-Detection—It might seem that all of the 'objective' factors in movement perception should be purely sensory, but there are certain ones which are chiefly motor in character—notably, the 'gyroscopic' action of the involuntary eye movements, under the control of the membranous labyrinth. This action tends to preserve the absolute orientation of the eyeball in space so that—as Erich Sachs puts it—"the head rotates around the eye" during the dynamic maintenance of equilibrium. This maintenance of ocular orientation makes toward a constancy of the visual field, whereas voluntary eye movements are designed to exchange the field and fixation-point for new ones.

If the eyes always turned with the head instead of automatically 'against' the head, the swimming of the visual field in a wholesale 'apparent movement' would conceal from the animal small real movements within the field. So many more parallactic relative movements would take place, that actually-moving objects would be harder to spot. The gyroscopic stabilization of the eye is a means of combatting the relativity of motion—by keeping the visual field still, the animal can better know what moves, when, and where.

Another motor phenomenon whose sensory accompaniments aid in movement-detection is the 'saccadic' eye movement. This is the type of voluntary eye movement which we make to change our point of fixation. During involuntary movement of the eyes, and during pursuit movements, we see continuously. But it is a striking fact, more than a little hard to believe, that we do not see at all during saccadic movements. Some sort of switch is opened in the brain, until the movement is completed. Then, vision returns. One simple proof of this is the fact that it is impossible to see the eyes in voluntary motion in a mirror. Another is Dodge's experiment: look at an object through the narrow apex of a paper cone, then look to one side of the aperture and sweep the line of sight across it. You will see nothing of the object, through the aperture, unless the line of sight stops upon it. We read a line of print not continuously but by jerks, seeing the words only in the moments when the eye is at rest. The fewer stops one makes per line, the faster a reader he

can be; and yet, the fewer stops one makes, the more time one is actually seeing the words.

If one holds the eyes motionless in the orbits and turns the head from side to side, vision is then continuous and one experiences the same 'swimming', or apparent movement of the whole field, that occurs during vertigo or intoxication when the reflex eye movements (during which vision is also continuous) are occurring in such an abnormal way that the 'gyroscope' is wobbly. But now if the head be kept still, and the eyes swept voluntarily from side to side through the same angle as before, the field does not swim because vision occurs only at the multiple stopping-points of the eye's discontinuous rotation.

Here again, in the suppression of vision during saccadic eye movements, we have a mechanism for maintaining a constancy of the direction of objects, so that if one of these *should* move, we will be better able to notice it. There seems to be no other reason why this kind of 'suppression' ever evolved. The chances are that in some animals whose eyes move but little or not at all, a similar suppression takes place during head movements, such as the perpetual fore-and-aft movement of a walking pigeon's head.

Beebe describes an experience he has had, while helmet-diving in shallow water, which demonstrates strikingly the relativity of movement for animals and their dependence upon a constant visual field for the recognition of movements. The movements of the water were causing the bottom vegetation to sway slowly to and fro. As long as Beebe swayed his body with the plants, the many fish in the neighborhood ignored his presence. But when he stood erect and motionless, the fish were immediately curious about him and came over to investigate.

Sensory Factors in Movement-Detection—Given a situation in which the background and motor factors are conducive to the perception of a movement, and do not tend to conceal it among apparent movements or to create a 'referred' movement (*i.e.*, cause the motion to be attributed to the wrong object), there are two principal sensory factors which come into play. These are visual acuity and the persistence-time. It is upon the value of each of these, in a given animal, that the demarcations between imperceptible and slow, medium, and fast perceptible movements will establish themselves for that kind of animal.

The dependence of movement perception upon visual acuity does not at first glance seem to be very direct. We can see an object, if it is in

motion, from a much greater distance than that from which we can resolve it if it is still. Ovio has given a simple explanation of this: If we take as our criterion of visual acuity the two-point limen, or angular separation which two points must have if they are to be just resolvable as separate points, then their subjective separateness is due to the fact that their images on the retina fall upon 'circles of innervation', or groups of visual cells (one in each 'group', in the fovea) connected with single optic nerve fibers, which have between them an unstimulated circle of innervation. The actual separation of the points in space thus corresponds, in the retinal image, to the diameter of a circle of innervation in that part of the retina. But now if the displacement of a single point in space is to be visible, the image of that point need move on the retina a distance equal only to the radius of a circle of innervation, in order to fall upon a new circle and register the displacement.

This idea is quite well borne out by the experimental facts. The two-point limen at the human fovea is about 40″ of arc. The angular displacement-threshold at the fovea is 20″ of arc or less, according to different observers. Schmid, studying the visual performance of fourteen police dogs, found that the best dogs could recognize moving objects at 810-900 meters, while the best record with the object stationary was 585 meters—not far from the 2:1 ratio which Ovio's explanation roughly predicts. Thus, paradoxically, it seems that we should, after all, discriminate changes in a visual pattern better than the static features of the pattern itself.

When a visual stimulus is presented, there is a 'latent period' before the sensation develops, and the sensation lasts longer than the presentation-time or duration of the stimulus. The 'persistence time' is the period within which a stimulus continues to be sensed after it has been removed. In vision, this period is synonymous with the duration of the 'immediate positive after-image' of a stimulus. It is commonly stated to be responsible for making motion pictures 'move', though it is directly involved only in the elimination of 'flicker' from them. If an after-image has not commenced to fade before an identical second stimulus evokes its full-strength sensation, the second sensation or impression will merge with the first. As successive flashes of light are thrown on the same retinal area, an increase in their frequency leads ultimately to the perception of a steadily-burning light, at the 'critical frequency of fusion'.

Now, at this critical frequency, the interval between the cessation of one stimulus and the commencement of the next might be called a

'refractory period', because no identical stimulus presented within this period can be perceived as separate from the preceding one. The period has been called by von Uexküll the 'biological moment'—the shortest discriminable unit of time for the animal. This name for it has justification only if it be found that in all sensory modalities the duration of the 'moment' is about the same. And, Uexküll did find very good agreement. Thus for example, a snail fuses visual impressions coming at four or five per second, and cannot distinguish mechanical taps on its foot, at this same frequency, from a steady pressure. We fuse movie frames at 16 per second, and the lowest frequency of auditory impulses which we fuse into a steady tone is also 16 per second. But, with each of the senses, the duration of the 'moment' is profoundly influenced both by the intensity of the stimulus and the adaptation-condition of the sense-organ.

We can now understand how the persistence time affects the perception of movements at different speeds. As an object moves slowly across the field we see it with the same clarity, at each instant, that we would if its image were motionless upon the part of the retina which it strikes at that instant. The after-images of the object are being given adequate time in which to fade. With increasing speed, the image of the object in a given position is overlapped by, and blurred by, the after-images of the object in its just-previous positions. We see this blur as movingness and, if the visual acuity of the particular retinal area is extremely low, the movingness may seem disembodied. If, now, the object traverses the entire field within the period of the persistence time, we will obviously see nothing *but* blur, and perhaps cannot decide the direction of the movement. And, if the object is of such brightness, and moves at such speed, that its image endures for too short a time on any one spot of retina to arouse any sensation, the flight of the object—a bullet, for instance—becomes supra-perceptible. But by enlarging or brightening the object (as with a howitzer shell, or a tracer bullet) we may restore visibility of its flight even at terrific speed.

A few years ago, quite a furore was created by the scientific announcement that a deer-fly can travel at 800 miles per hour. Skepticism took various forms. A biochemist computed that the fly would consume its own weight in food every hundred yards or so at such a level of muscular activity. Langmuir, of the General Electric Company, noting that the deer-fly at its speediest is still visible, swung a fly-sized lead pellet at the end of a wire at known speeds. When the linear speed of the pellet was 13 miles per hour, the pellet was blurred. At 26 miles per hour it was

barely visible as a moving object. At 43, it became a faint line whose direction could not be recognized; and at 64 miles per hour it was wholly invisible.

It is sometimes given, as a characteristic of true movement perception, that we do not see the object in all of its intermediate positions. That really depends upon the nature of the object. The body of an automobile may be seen clearly at all points in a movement at a given speed. But the tops of the wheels are travelling faster than the car itself, and so the wheels may blur. Before the invention of the motion-picture camera, a famous photographer, Eadweard Muybridge, made photographic studies of the gait of running horses at the behest of a group of sportsmen who wanted to settle an argument as to whether a trotting horse ever has all four feet off the ground at once. Muybridge used as many as forty automatic cameras spaced along the track. When some of his pictures were handed to horsemen, they refused to believe that a horse's legs ever get into some of the positions shown in the photos. But they were forgetting that while the horse's body cannot travel too fast to be seen clearly, its legs in their forward movements travel so much faster than the horse that they blur in human vision, and no one can honestly say that he sees them in all their positions. While the eye is following the horse's body by a pursuit movement, it cannot very well follow, at the same time, the movements of the horse's legs.

Adaptation, and Center versus Periphery—The higher the visual acuity, the lower the angular displacement threshold—hence, the better a moving object can be seen and the smaller a movement can be detected. The higher the critical frequency for fusion, the shorter the persistence time (and, sometimes, the latent period)—hence, the less the blur of a moving object and the faster it can move and still be seen well as to its nature, direction, and velocity.

Visual acuity and critical frequency, being fairly easy to determine in man and animals, are thus our best criteria of the comparative objective capacities of vertebrates for movement-perception. But both of these values are very different for the cone-mechanism and rod-mechanism of the retina. In the average retina (one which is duplex and has an area centralis) both values are profoundly influenced by the conditions of light- and dark-adaptation and by the differing concentration of rods and cones in the center of the retina as contrasted with the periphery.

It is generally believed that movements are better seen peripherally than centrally. The situation with regard to the objective (*i.e.*, physi-

ological) factors does not bear this out. But the psychic factors are largely in favor of the periphery, in which movements have a saliency and attention-value quite out of proportion to the clarity with which they are actually discriminated. We might think that this was a compensation for the inferior capacity of the periphery to detect movements; but a moment's reflection shows that there could be no such compensation, any more than increasing the strength of our brightness-sensations could of itself make the eye more sensitive to weaker lights.

So, when the retinal periphery is described as "an organ which is specially adapted to see movement", we need to append: "so far as psychic factors are concerned." Animals with panoramic vision, animals which like the horse have greatly extended peripheries and wide visual angles, and animals like the mouse with pure-rod retinæ (which can be thought of as 'all periphery'), are *not* specially equipped to discriminate movement and moving objects. If in the rat's whole retina, or in the ungulate's periphery, visual acuity is so low that only movingness, not moving objects, can be seen, it is not that these retinal areas are designed for movement-perception—rather, it is that they are too crude to afford any phases of vision *except* movingness and brightness. What movements the animal does pick up may startle him more than they would a lizard or a man; but this is a matter of saliency, the biological need or lack of need for which varies from species to species. Lizards and men are better able to identify a moving object promptly, and are therefore not under the necessity of treating every moving object which enters the visual field as a dangerous enemy until it proves itself otherwise.

Certainly, as Woodworth says, the brain is tuned to see motion and grasps at any chance to see it. That is doubly true when the brain is peering out at the world through the periphery of the retina. Even the momentary stimulation of the periphery by a spot of light is said to cause an impression of movement. A moving point in the periphery is more visible than a line of similar length, direction, and duration. There are two factors which operate to promote movement-detection in the periphery. One of these is quite important, and gives a moving object a sort of physiological saliency which may indeed be a large part of the basis of psychic saliency. This is the great 'fatigibility' of the periphery. Motionless objects in the periphery of the visual field actually tend, from this cause, to disappear after a few moments. But now if one of them begins to move, it is immediately seen again, since its image passes over retinal areas which have meanwhile become adapted to other images but

are responsive to any change. Another, and minor, advantage of the periphery which depends upon the morphology of the eye (actually, upon one of its so-called imperfections) is the 'barrel distortion' of the peripheral field: as a circular image swings steadily outwards along a meridian of the retina into the far periphery, it becomes elliptical with its long axis meridionally oriented. If two such images move together into the periphery, hailing from two objects whose separation in space remains constant, the distance between the images (hence, the disparity between their apparent relative speeds) increases along with the distortion. We may not be conscious of any peripheral aberration of shapes under ordinary conditions; but nevertheless peripheral movements, in meridional directions at least, are optically exaggerated to a not unimportant degree by this increased speed of the sweep of the image over the retina. In some animals' eyes, where the retina is broadened in the horizontal meridian by an ellipticity of the eyeball (horse, swift fishes), this factor may be quite important.

Many more factors, however, operate to the disadvantage of the periphery in movement-detection. Foremost of these is the rapid fall of visual acuity from center to periphery, which is an expression of the increasing size, meridionally outward, of the circles of innervation. The acuity of displacement-discrimination also falls from center to periphery, though not as rapidly as does the resolving power. In light-adaptation, when central (*i.e.,* cone) vision is at its best, the central fusion-frequency is higher than in dark-adaptation; and, of course, visual acuity also rises with intensity. In dark-adaptation, where the rods are under optimal conditions, acuity is low; but it so happens that the peripheral critical frequency is higher than it is in light-adaptation. In a duplex retina under any given adaptation-condition, the central acuity and critical frequency are ordinarily higher than the corresponding peripheral values. The higher the illumination, the farther peripherally a movement of a given speed is appreciated, due to the cones coming into play. When the periphery is dark-adapted, however, it may still record flicker when this has disappeared for a partly light-adapted center. One can experience this at the movies, where the screen is flickerless but a hand moved across the lap (while the screen is fixated) is seen intermittently.

Similarly, rod-rich retinæ (cat, owl) have been found to have lower critical frequencies than cone-rich ones (pigeon) in the same condition of adaptation. We cannot compare with perfect fairness the light-adapted central vision and dark-adapted peripheral vision of a duplex retina with,

respectively, pure-cone and pure-rod retinæ under their respective optimal conditions; for there are mysterious mutual inhibitory effects of the rod- and cone-mechanisms of a duplex retina. But, from the data on critical frequencies at least, we may suggest that a diurnal animal has his best movement-perception in the daytime while a more rod-rich, nocturnal, animal sees movements better at night than by day. In pure or simplex retinæ, acuity-differences between the light-adapted and dark-adapted conditions are probably slight as compared with the differences in visual acuity between light-adapted duplex retinæ and dark-adapted ones; so, in both pure-cone and pure-rod animals, the adaptation-state probably influences movement-perception chiefly through its effect on fusion-frequency. When both diurnal and nocturnal animals are adapted to the same illumination however, we should expect the movement-perception of the diurnal form to be always superior on the grounds of both the visual acuity and persistence-time factors.

Other factors militating against the periphery are its poor performances in the matter of discriminating hues and the discrimination of intensities. Both of these capacities are involved in visual acuity in its broad sense—that is, in the perception of pattern, and consequently of the changes of pattern which result from movements. Farther and farther peripherally, fewer and fewer hues, less and less saturated, are seen. At least, this is true of man, and probably of all color-perceptive vertebrates. And, the discrimination of intensities (and hence, of contours between areas of different objective luminosity) is much poorer peripherally than centrally, and poorer in dark-adaptation than in light-adaptation. As a consequence, it is found that movements are perceived farther into the periphery, and more easily, when the background is made brighter to give the object more contrast.

Wavelength as such can also influence movement-perception, presumably even in animals which have no color vision; for the critical frequency differs for different hues of light. A Swedish railroad recently found that certain red signals, which had to be seen as blinking, could be so seen if they flashed 75 times per minute. Blue ones could be allowed to flash only 20 times per minute, else there was danger of fusion by the dark-adapted eye of the engineer.

We cannot say very much about the basis of the saliency of movements, even in human vision. The apparent rate of a movement is almost twice as great if some stationary object is fixated, as when a moving object is pursued by the eye. Probably this is due to the fact that in the

first case the blur of movingness is attached to the object, while in the second case the object is clearer—therefore less 'moving'; and also the blur of the shifting background, being out of focus to begin with (since the eye is accommodating for the object) is less prominent in consciousness. Still, even with steady fixation, movements seem two or three times as fast when seen peripherally as they do in direct vision.

Not all perceptual factors promote saliency, however—some have a reverse effect. If two lights are flashed simultaneously just once, one being seen centrally and the other peripherally, they appear to flash in succession with the central light leading the other. The latent period of perception is thus longer in the periphery. A French worker has studied the whole sensorimotor reaction time with central versus peripheral vision and with the motor elements constant. A chronoscope was used, whose indicating hand could be started moving by the experimenter and stopped by the subject's pressing a key as soon as he was aware of the movement. On the average, the whole reaction time with central observation was 0.170 seconds, while at 90° in the periphery it was extended to 0.327 seconds. This means that an object would have time to move farther in the periphery, as compared with the center of the field, before the individual could take any motor action upon the matter.

On the whole, it would seem that the periphery exercises its greatest usefulness in movement-perception by instigating the reflex 'eye-jump' which calls the visual axis over to aim at the locus of the movement. This reflex is very strong, even in civilized man, who should theoretically have very few primitive fear-reflexes left. It may not occur when the peripheral movements are expected or at least not unexpected; but a man in strange surroundings will inevitably turn his eyes—the first time, at least—to see foveally a waving window-curtain or what not, which has 'caught his eye' peripherally.

Stroboscopic Movement versus Real Movement—There are many kinds of apparent movements—perceptions of movement where the object to which the motion is attributed is actually stationary. Most of these have their basis in movements of the eyes, or of the head, of which the subject is unaware—the visual axis swinging, though the subject believes his fixation to be constant. Any disturbance of egocentric localization, as in vertigo and intoxication, results in a swimming apparent movement of the whole field. In another category are after-images of motion, where both the eye and the apparently moving object are station-

ary. One experiences this illusion after watching a waterfall or a stream for a time, and then turning one's attention to objects on the bank.

The third, most important and most interesting kind of apparent movement is that called variously stroboscopic or cinematoscopic movement, or the 'ϕ-phenomenon'. It is obtained either when identical or slightly differing images fall in succession upon neighboring retinal areas, or when slightly different images fall successively on the same retinal spot.

The stroboscope (meaning 'whirling looker') was invented almost simultaneously by Plateau and Stampfer more than a century ago. In any of its many forms, it is a device for making moving objects appear to be stationary, where the object—usually a rotating one—has a regular and serially-repeated pattern. The reader can make a simple stroboscope (see Fig. 125a) in the following way: Take a disc of cardboard about

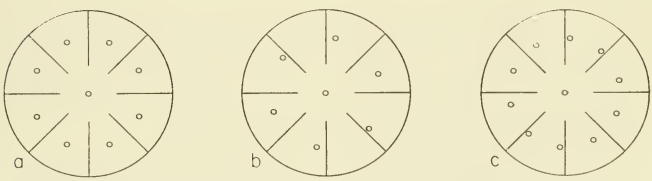

Fig. 125—Simple stroboscopes (see text).

eight inches in diameter and puncture its center with a pencil which can then serve as an axle. Draw a few radial pencil lines on the disc, evenly spaced. Punch small holes through or between these radii, equal in number to the latter, equally spaced apart, and equidistant from the center. Now place the disc with the pencilled radii facing a mirror, and, with the eye looking into the mirror through one of the small holes, spin the disc.

One sees the pattern of pencil lines 'standing still', like the spokes of a motionless wheel, no matter what the speed of the disc. The eye sees the group of lines reflected in the mirror every time a hole comes along, but the small hole permits such a brief glimpse that no motion of the lines is perceptible. Since, through each hole, lines are always to be seen pointing in the same set of directions, only this single changeless pattern can be seen.

The higher the speed, the smaller the holes must be to 'stop' the motion, until impracticably small holes are required. In stroboscopy in industry, for seeing the distortions of rapidly rotating parts, intermittent illumination is more feasible. If a motor armature is whirling at ten thousand revolutions per minute, and is illuminated by ten thousand light-flashes per minute, each of very short duration, the armature is seen as if standing still; but any distortions produced by its rotation are visible and can be studied deliberately.

Now, if our cardboard disc should have one or two more evenly-spaced radii than the number of evenly-spaced holes (Fig. 125b), the pencilled pattern will appear to rotate slowly forward. If the number of holes is in excess (Fig. 125c), the spokes will seem to turn slowly backward. These apparent movements of a pattern which (seen through any one small hole) is always actually motionless, are stroboscopic apparent movements.

We can duplicate the essentials of this illusion in a darkroom with a pair of small lights. If the two lights are a given distance apart and of a given intensity, and are flashed in succession, there will be found a time-interval of flashing at which one sees the first light apparently slide over into the position of the second. Between the two end positions of this 'single' light, a distinct blur of movingness is seen.

If the time interval between the two flashes is too long, however, one sees two lights flashing in sequence with no illusion of movement. This is called the 'successive phase' of the illusion. Shortening the time interval now brings back the optimal phase, in which the movement is perceived. With very short time intervals, the 'simultaneous phase' is reached, in which the two lights appear to flash together.

This illusion is called the ϕ-phenomenon. The movement seen need not be in a straight line—it always follows a course which it might be 'expected' to do. Thus, if the two stimulus-spots are both tangent to a visible curved line, the first spot seems actually to roll along the curve to reach the position of the second stimulus. If the two stimuli are lines which, if presented simultaneously, would form a right angle, the appearance seen in the optimal phase is of a single line pivoted at one end and swinging through a right angle (Fig. 126).

The ϕ-phenomenon sounds academic when thus described in terms of unfamiliar apparatus, but we experience it about 200,000 times whenever we sit through a movie show. It is the ϕ-phenomenon which makes the movies move, for the motion picture camera is like our stroboscope with

fewer holes than spokes. Each time the shutter opens to expose a frame on the momentarily motionless film, the objects in the field are in new positions, displaced a bit from their previous ones at the last opening of the shutter 1/20 of a second or so ago. Projected at the same frequency of frames-per-second, the spatial intervals between the successive positions of the screen images are filled in subjectively with the same movingness we experience with our pair of flashing lights.

The ϕ-phenomenon is closely related to the perception of real movement, but the two are not identical psychological processes. Rather, they are children of the same mother, whose name is persistence time. To have the optimal phase of the ϕ-phenomenon with, say, our two lights, the second stimulus must appear at about the same instant that the impression of the first fades. If the second stimulus comes late, the successive

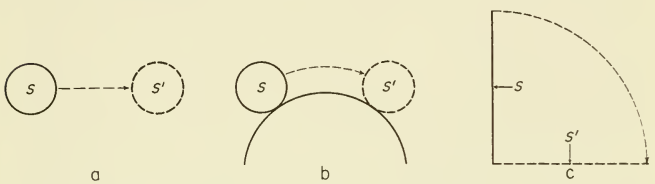

Fig. 126—Versions of the phi-phenomenon.

a, the simplest situation: when stimulus *s* is presented, then *s'*, the subject sees *s* apparently move over into the position of *s'*. b, if, in order actually to move to the position of *s'*, *s* would have to follow a curve, then the apparent movement of *s* will be seen by the subject to take the appropriate curved course. c, if, in order actually to move to the position of *s'*, *s* would have to pivot, then in its apparent movement it is perceived as doing so.

phase supervenes; and, if the second stimulus comes too soon, the simultaneous phase sets in. Harking back to our classification of the perceptions of real movements (pp. 346-7) and the influence of the persistence time upon them, it is easy to see that slow movements correspond to the successive phase, medium movements to the optimal phase, and fast movements to the simultaneous phase of the ϕ-phenomenon.

This common dependence of movingness, in both real and stroboscopic movements, upon the critical frequency of fusion has led to two beliefs. Cermak once pointed out that if the two lights in the ϕ-phenomenon were alternated in the optimal phase, and the distance between them reduced to zero, one would have a single flickering light. With the rate of alternation then raised to correspond to the simultaneous phase, the two

lights at zero distance would fuse into a single steady light. Many workers have drawn the conclusion that our mechanism for apparent-movement perception may be the only one we have with which to perceive *real* movement. The 'laws of Korte', which express the interrelations of the time interval, spatial separation, and intensity of stimuli for the optimal ϕ-phenomenon, also hold very well for the perception of real movements. That is, if a third light of the same intensity is really moved, within the same time, parallel to the two lights used for the ϕ-phenomenon, the real and apparent movements are seen alike. Speeded up to the short interval of the simultaneous phase, the real movement becomes a line of light without direction. Slowed down to simulate the successive phase, the really-moving light loses its blur of movingness.

Another common belief is that the movement of the movies is solely created by projection at the speed of the critical frequency. Since both the elimination of flicker and the optimal ϕ-phenomenon depend upon this speed of projection, the conclusion that they are identical seems plausible. But it is easily possible to separate the conditions for the optimal ϕ-phenomenon from the conditions for the elimination of flicker. Suppose we print every twentieth frame of the negative on successive frames of a positive film, and project it at the usual speed. There will be no flicker—but the spatial separations in the images will be so great that only jerky movements or successively new positions, with no smooth movingness, will be seen.

We need not produce such a film intentionally. It happened as an unfortunate accident in the making of Walt Disney's *Snow-White and the Seven Dwarfs*. The slow movements of the human characters seemed unpleasantly jerky on the screen. The faster movements of the little animals were just as jerky, but were quite acceptable to the onlooker; for when we watch a real chipmunk skip about we do not actually see him when he is in motion. Human movements are so much slower that the loss of movingness, due to too great spatial separation of the successive drawings of the animation, was 'unnatural'. Disney pushed the ϕ-phenomenon a little too far; and to obtain any more satisfactory illusion of human movements in animated cartoons, it is absolutely necessary to draw just as many intermediate stages in each movement as there would be on a motion-picture film of an actual human movement of the same speed. While watching any ordinary movie, one can hold a finger in front of the eyes and sweep it across the angle subtended by the screen much faster than an object of the same apparent size would ever move

across the field of the camera. When this is done, the finger is seen to jerk across the screen, taking twenty new positions per second, and does not appear to be in motion at all.

Before we leave the movies, it is worth-while to point out that the ϕ-phenomenon can be seen binocularly. A real movement appears just as continuous if we blink our eyes alternately while observing it. So also, the ϕ-phenomenon occurs if each eye sees only one of the stimuli. A movie will still move even if shutters placed before the two eyes are opened and closed alternately in synchrony with the alternate frames of the film—it is only necessary to take and project the picture at twice-normal speed, to prevent flicker. This phenomenon is the basis of some methods of making stereoscopic motion pictures.

A common illustration of the ϕ-phenomenon, often suggested in psychological text books because it requires no apparatus and is therefore 'simple', is actually of the binocular type—with special complications: if a finger is held still before the eyes, and the eyes are blinked alternately, the finger is seen to move from side to side. Actually, the single finger cannot represent our pair of ϕ-phenomenon lights—it appears in two positions, to begin with, only if we are accommodating beyond it. The two diplopic images of the finger then have different apparent positions because of their different parallaxes with background objects. If one accommodates and converges steadily upon the finger, it will not 'move' at all when the eyes are alternated. Blinking the eyes makes it difficult to maintain the convergence for the finger. Try propping up a pencil instead, and occluding the eyes alternately with your hands, held before them, while watching the pencil. The pencil will not 'move', unless you fixate something *beyond* it.

Now, can the machinery with which we see real movements be, actually, our machinery for stroboscopic perception? When the distance and duration of real and apparent movements is objectively the same, they appear equally moving; but the real movement may seem slower and smoother and the apparent movement a bit jerky. This jerkiness we can attribute to the fact that the impact of the second stimulus upon its retinal spot is sudden. The relative retardation of the real movement is perhaps due to the circumstance that intermediate retinal areas are actually receiving stimulation; for, as is well-known, we see an occupied space as longer than an unoccupied one, and if a movement traverses the two in the same time, it will seem to traverse the occupied space more slowly.

But there is another difference between the two percepts which cannot be explained away and cannot be reconciled with the idea of a completely identical basis for the two. The movingnesses seen in both cases may seem much alike, but they have utterly different sources. In real motion, the movingness-blur is of physiological origin, and resides in the retina. The overlapped photochemical images which produce it are chronologically older than the foremost, newest image of the moving object. But in the ϕ-phenomenon it is obvious that the generation of the movingness cannot possibly commence in the brain until after the retina has been hit by the second light—otherwise, what would determine the direction the movingness was to take? In some way however, the impression of motion reaches consciousness *before* the impression of the final position of the movement—the second light—gets there. The phsysiological sequence of events is: (*a*) reception of the first light; (*b*) reception of the second light; (*c*) instigation of the filling-in process, the percept of movingness. But the *perceptual* sequence is: (*a*) light in initial position; (*b*) movingness; (*c*) light in its final position.

Real and stroboscopic movements are thus deceptively similar subjectively; but the only things they share in common objectively are their dependence upon similar conditions of brightness and distance, and the rôle played in each by the persistence time. This is probably not a coincidence, for the close imitation of real movement by apparent movement under the same spatial, temporal, and intensity-conditions presumably has some biological value. What it is, we cannot say. The writer would suggest—most gingerly!—that perhaps when a primitive, stupid vertebrate saw a moving object pass behind an obstacle and emerge again, he could not be trusted to know that it was all one object, and not two different ones, unless he had an automatic means of maintaining the oneness of the object during the moment when it was hidden from him. Whatever the incentive may have been for the evolution of the 'filling-in' process in the ϕ-phenomenon, it is difficult to see what good its retention has done *us*—unless one belongs to the growing number who regard the movies as an absolute necessity.

Stroboscopic Vision in Animals—It is fairly certain that the lower animals in general do have perception of stroboscopic apparent movement. At least, it is well established experimentally for fishes and can be inferred from such phenomena as the dog's interest in, and obvious deception by, motion pictures, coupled with his complete indifference toward still pictures. If apparent-movement perception exists for the

fishes, it probably exists all the way up to the dog and man. There appears no positive reason why it should have been eliminated by any particular group, though it must be admitted that its usefulness is obscure.

The scanty experimental work indicates that stroboscopic movement is seen by animals, as by man, as practically indistinguishable from real movement of an equally luminous object over the same distance in the same time. If further work is done along this line, and shows this rule of 'identity' to hold firmly in case after case, we shall have a powerful experimental tool for exploring animal capacity for real-movement perception; for, as a matter of technical convenience, the ϕ-phenomenon is more easily presented to an animal than is an equivalent real movement. The apparatus is simple, and the control of such factors as accompanying noise is much easier. Variations are more easily introduced, for it is far simpler to space two lights farther apart than to alter machinery which moves one light back and forth.

A few years ago, Mlle. Gaffron demonstrated stroboscopic vision in two fishes, *Phoxinus lævis* and *Gasterosteus aculeatus,* though with the same technique she could find no evidence of it in various insects. The dish containing the fish was surrounded by a cylinder capable of rotation on a vertical axis and bearing vertical stripes on its inner surface. Rotated slowly in either direction, the cylinder naturally evoked the optomotor reaction—the fishes either swimming around with it or turning into a radial position in which the eyes alone followed the movement. When the cylinder was now illuminated intermittently, at different frequencies, the fish responded to it as if it were motionless, or turning in its actual direction, or turning in the opposite of its real direction, depending upon the timing of the flashes relative to the positions of the stripes. Interestingly enough, the apparent motionlessness, forward movement, and apparent reversal of the cylinder were each seen by human observers under the same conditions as by the fishes.

Almost simultaneously, von Schiller published his researches on the stroboscopic vision of *Phoxinus*. He used a form of the ϕ-phenomenon situation in which two white squares, set one above the other with a certain separation, could be revealed at one end of the aquarium for various periods and in succession at various time intervals. The fishes were initially trained positive to an actual upward movement of a similar white square, which was made a signal for food. Presented then with the ϕ-phenomenon, with the object, duration, and distance all identical with the real movement to which they had been trained, the fishes responded

as if they were witnessing the real movement. The real and apparent movements were completely interchangeable for them.

Moreover, Schiller was able to induce negative responses by lengthening or shortening the interval between the presentations of the two white squares. When human observers were experiencing the successive or simultaneous phases of the illusion, the fishes were negative. Within the range of the optimal phase for humans, the fishes responded positively. Schiller concluded that the three phases exist for *Phoxinus* and for man under identical conditions. This would seem to imply that both species have the same persistence time, at least under the adaptation-conditions of the experiments.

Mlle. Gaffron and Schiller both stress the fact that the fishes have no cerebral cortex, and that therefore they (and man?) must 'see' apparent movement with some lower visual center. Schiller believes further that the mechanisms for real- and apparent-movement perception must be one and the same, and suggests that in apparent movement we "see with unstimulated parts of the retina." Since intermediate parts of the retina need not be stimulated in a real movement in order to perceive the movement, Schiller goes so far as to say that it is incorrect to call stroboscopic movement an *apparent* movement—it is as real as any other, physiologically. But, though the movingness of this phenomenon is perhaps registered in man somewhere below the visual cortex, it is the blurred train of after-images—assuredly registered in the cortex—which puts movingness into the percept of a real movement of our 'medium' category.*

The identity of persistence times in *Phoxinus* and man seems to be an accident. In the Siamese fighting-fish, *Betta splendens,* Beniuc found a much shorter period. He cleverly demonstrated both the biological moment and the existence of complementary colors for this fish in a single experiment. The fishes were trained positive to a gray disc and negative to a slowly revolving disc whose six sectors were alternately of two colors which are complementary for humans, yielding gray when mixed by rapid rotation.

When the disc rotated at a speed at which its sectors gave the fish 130 impressions per second, the fish responded to it as if it were the motionless gray disc. Beniuc found that at 90 impressions per second

*Pötzl has described psychiatric cases in which the movingness of real movements was not seen. A moving light was perceived as several lights in a series of positions—for all the world like the appearance of a phi-phenomenon, in its successive phase, to a normal person. It is impossible to say just what part of the normal equipment is lacking in such individuals.

(far above human fusion frequency) the fish was still clearly perceiving the rotation. At 100-120, the fishes reacted poorly, and were probably experiencing flicker. 110 impressions per second was the lowest limit for fusion. Beniuc translated this figure into a value of 1/55 second for the duration of the biological moment of the Siamese fighting-fish.

Menner's Theory of the Pecten—The pecten of the bird eye (see Figs. 80, 114; pp. 188, 308) has been one of the greatest puzzles in comparative ophthalmology. Some years ago an authority counted over thirty theories as to its function, which were sufficiently different to call distinct interpretations. Other suggestions have been made since, but none more intriguing than the very recent one offered by Erich Menner.

The pecten (Fig. 114, p. 308) is a simple cone in reptiles, where it cannot possibly play a rôle in vision but is merely a nutritive organ, on a par with the falciform processes, retinal vessels, and chorioid 'glands'

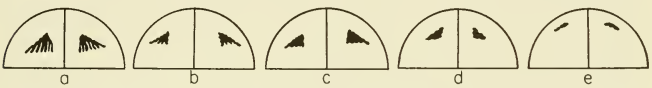

Fig. 127—Overall tracings of the shadows cast by the pecten in each eye, in various species of birds, in relation to their feeding habits and their consequent needs with regard to movement-perception. After Menner.

a, *Buteo buteo* (a hawk, feeding largely on cursorial prey). b, Coal titmouse, *Parus ater* (chiefly insectivorous). c, English sparrow, *Passer domesticus* (chiefly granivorous). d, Domestic pigeon, *Columba livia* (granivorous). e, Long-eared owl, *Asio otus* (predaceous, but largely dependent upon audition).

of other vertebrate categories. In birds, however, it is an elaborately pleated fin of pigmented and richly vascular tissue, reaching from the retina nearly to the lens (Chapter 17). One can account for its great increase of surface, over that of the reptilian organ, on the basis of the bird's warm-bloodedness and elevated metabolism. But ulterior meanings of this conspicuous organ have long been sought, the search stimulated by the enormous variability of the pecten from species to species, and by the hope of correlating these variations with something else in the visual biology of birds. Briefly, the pecten is smallest, with the fewest pleats, in nocturnal birds. It is larger in seminivorous forms, still larger and more elaborate in insectivorous birds, and largest of all in the diurnal predators such as the hawks and eagles.

Menner placed numerous bird heads in a special perimeter and studied the pecten with the ophthalmoscope from many angles. He found that

the pecten casts a shadow on the retina and that the tips of its pleats extend this shadow, like the fingers of a hand, across the fundus and the neighborhood of the area centralis. Figure 127 shows sample over-all shadows—composite sketches made with many directions of the ophthalmoscope light, from birds representative of various categories.

Menner felt that the dactyloid shadows of the pleats might be a device for enhancing the perceptibility of movements. To test this idea he aimed a camera, focused for infinity, at some circling birds in the sky. On the ground-glass screen, nothing could be seen. He now glued to the inside of the glass a cardboard model of the pecten which would cast finger-like shadows. With the camera pointed again at the wheeling birds, their movements and courses were at once evident upon the screen.

The phenomenon was then explained in terms of some old statements of Exner, who found that a movement was especially conspicuous when the image swung back and forth across the blind spot—the head of the optic nerve. The repeated 'on' and 'off' effects gave the movement greater saliency in consciousness. Menner decided that the multiplicity of pecten-pleat shadows must do the same thing, in a big way: each shadow, if pronounced (*i.e.*, in strong illumination) would create a temporary blind spot or streak, over which the swinging image would have on-and-off impacts on the retina and in consciousness. He pointed out that the development of the pecten in different birds (*v.s.*) goes hand in hand with their need, considering their feeding habits, of good visual movement-perception.

It had long since been decided by others that the development of the pecten in various birds is correlated with their ranges of accommodation, though no one has demonstrated that the pecten plays any part in the process of accommodation in birds or reptiles. Now of course good accommodation, high visual acuity, and acute movement-discrimination would all be expected to go together in birds anyway—all being lowest in the owls, highest in the hawks, with the granivorous birds and the bug-eaters fitting neatly in between. These correlations do exist; and so, as far as Menner's theory is concerned, the relationship he points to (between pecten and habits) would exist whether his theory has any value or not. The different ecological types of birds do need different movement-seeing abilities, but their visual acuities alone, and their persistence times, are probably already related nicely to their needs in this respect without taking the pecten into account at all.

It is not entirely certain that the pecten, which is always located

ventrally along the course of the embryonic fissure (see p. 107) ever casts a shadow on the fundus at all unless the bird looks up at the sky. The shadow may not often be very useful in terms of Menner's hypothesis; and, assuming that there usually is a shadow, it may not operate entirely as Menner believes it to. Any moving object—the object itself, not its motion—should be seen more clearly if seen intermittently. One can often count the blades of a rotating electric fan by blinking the eyes rapidly so that each glimpse is only momentary. This, in fact, is the very essence of stroboscopy—everyone knows that it takes a fast camera shutter to 'stop' fast motion.

If a moving object is seen only intermittently, its nature can be better made out since each image of it on the retina is less blurred by dragged after-images. But it does not seem as if the fingers of a pecten shadow are numerous enough and sufficiently close together to afford a series of snap-shots of a moving object, analogous to those obtained by Eadweard Muybridge's row of cameras. And if they were, they would hinder vision in general for the bird, which would hardly benefit from being made to look at the world as if through a picket fence. But if there is anything to Menner's theory, it may help to explain another peculiarity of ocular structure: multiple optic papillæ.

Multiple Optic Papillæ—In a number of fishes (for example *Ameiurus, Misgurnus, Polyipnus,* and *Polypterus*), in various salamanders, and in members of the deer family, the optic nerve on approaching the eyeball divides into as many as a dozen or more separate rootlets, forming an equal number of separate little blind spots with functional retinal tissue around and between them. In the squirrels (pp. 179-80) we saw a deformation of the blind spot which is intended to minimize the scotoma effect, thus promoting overall visual acuity. The situation in the Cervidæ may have this same meaning. But the multiple blind spots, which look as though they might have the same purpose of avoiding a single huge scotoma, mostly occur in forms with abysmally low visual acuity. Of the fishes listed above, *Polyipnus* is a deep-sea form, and none of the others has much, visually, beyond brightness- and movement-perception. Such animals have not needed the break-up of their blind spots to enable them to see more sharply, for they are beyond any such help. But if a turning on and off of the reception of a moving retinal image helps the movement to break into their dull minds, the multiple papillæ may do for them what Menner thinks the pecten does for the birds.

Chapter 11

ADAPTATIONS TO MEDIA AND SUBSTRATES

(A) Aquatic Vision

Definition—Before we consider the requirements and consequences of seeing through water we need to decide what we mean by aquatic in this connection. There is no doubt that all but a few fishes are aquatic; but one may read in one book that the seal is an aquatic mammal, and in another that he is an amphibious vertebrate. We may have to be a little arbitrary about our definition of 'aquatic', arriving at it by a process of elimination, and justifying our arbitrariness only in a later section.

The Amphibia (*amphi* = both, *bios* = life) were given their name because they spend part of their lives in water and part on land. The word amphibian means a member of the Class Amphibia. It is sometimes used as an adjective, but should be avoided in favor of *amphibious*. This word is much older than the scientific term Amphibia, and does not really connote the same thing at all. Amphibious animals are those which are in and out of the water off and on as an everyday thing, and 'equally at home' in both media. Very few members of the Amphibia behave at all in this way. Most of the common frogs (family Ranidæ) do. The less familiar but much more numerous tree-frogs, toads, and land salamanders do not. Most amphibians, then, are not amphibious. Rather, they are aquatic for a part of their life-cycles (as tadpoles) and terrestrial for the remainder with only brief annual visits to water to breed. Some salamanders and a few anurans (*e.g., Pipa* and *Xenopus* spp., *Telmatobius microphthalmus*) never leave the water—they are as aquatic as any fish. A few anurans (*e.g., Hyla zeteki*) never enter ponds or streams, their eggs developing in mere spoonfuls of water between the leaves, or in the central core, of bromeliad plants; and these forms are as terrestrial as a human—whose embryo, inside the amnion, also floats in water. The salamanders *Hydromantes italicus* and *Oedipus adspersus* are thoroughly terrestrial, and give birth to their young.

We shall consider as aquatic, then, those vertebrates which never leave the water. These animals with strictly aquatic *vision* include nearly all fishes, some amphibians, the sea-cows, and the whales. It so happens that

few of these ever even put their heads out of water for more than a moment, and are not then demonstrably trying to see through air.

These animals which fit our definition can be expected to have no compromises in their eyes, and to have these organs wholly devoted to seeing through water. But we do not know what to expect from the eye of any amphibious vertebrate until we learn whether he uses his eyes more in one medium or in the other, or equally in both. Many of the adaptations discussed in this section naturally occur in some or in full degree in the few amphibious fishes, as also in the amphibious species which are to be found in every order of the classes of amphibians and reptiles, and in many orders of both birds and mammals. Those losses and new acquisitions involved in the restriction of vision to the aërial medium are dealt with in the succeeding section of this chapter; and the particularly stringent ocular requirements of any animal which attempts 'amphibious' vision are considered in the third section.

Effect of Water upon the Plan of the Eye—It must never be forgotten that the vertebrate eye originated in water. Only when this is firmly in mind can we grasp the full meaning of some of the most fundamental features of ocular anatomy and physiology. When the vertebrates finally took the eye on land with them, they had perforce to fill it and surround it with simulations of its original medium of action, salt water—even as the spiders, coming to the land, remained dependent upon a bit of their old environment which they bottled up in their gill chambers.

Most of the physical and chemical properties of water affect the eye or its operation. Many of these properties are essentially simple exaggerations of those of air—the greater absorption of light, greater scattering, greater pressure-changes with altitude or depth, greater friction and so on. But the quantitative disparity between air and water, with respect to a given property, is so very great that in its evolution the aquatic eye responds qualitatively to factors whose air equivalents are negligible to it and evoke no adaptive response at all.

Before the evolving eye produced any precise adjustments to the purely optical properties of water, it had first to attain harmony with properties which affect all animal organs and tissues exposed to that medium, whether they are photosensory or not. The phenomenon which unquestionably had a more profound effect than any other upon the fundamental design of the vertebrate eye was *osmosis,* which therefore receives first consideration in our discussion.

When the two sides of a living membrane are bathed by liquids containing differing amounts of dissolved substances, there is a net flow of water through the membrane toward the side of the higher concentration. The easy way for a living cell, or a whole organism, to maintain its water content is to take advantage of this fact and expose its salty protoplasm to plain water, with a semi-permeable membrane intervening. A freshwater organism therefore need not drink water, for plenty of it is penetrating his surface continuously under the drive of osmosis. But in getting his water in this way the animal is literally playing with explosives. Unless controlled in some way (usually by excreting water about as fast as it comes in) the pressure built up inside the cells by osmosis will carry them past the desirable degree of turgidity, and will burst them. The freshwater organism has this problem of osmosis-control more urgently than the marine organism, for the disparity of concentrations of dissolved substances within and outside the body is far greater. Moreover, the freshwater form must provide against the loss of essential salts in the excreted water. We know, however, that the ancient seas were far less salty. While it is often said that the vertebrate blood was originally entrapped sea-water (the concentrations of salts in human blood therefore supposedly portraying the chemical pattern of the Devonian ocean) we may be sure that the protoplasms of marine animals of the remote past had higher osmotic pressures than that of the water outside—it would have been disastrous for protoplasm to have become otherwise. There is considerable evidence that the first vertebrates arose in fresh water, and we can be quite sure that the land animals evolved from freshwater fishes. Even at the present time it is the marine fish, not the freshwater one, which exhibits special devices in connection with the control of water-balance.

The rigidity of the vertebrate eye, which makes it a good optical instrument despite its constitution from soft and flexible tissues, is due to a bit of hydraulic trickery. The eye owes its firmness to the fact that it has a flexible but inelastic capsule which is kept distended by fluid pressure. The same principle makes a hollow tennis ball just as firm as a solid handball, and would allow us, if it were necessary, to put mobile objects inside the tennis ball—a point which will seem important in a moment.

The primeval source of this distensive intra-ocular pressure was osmosis. Some excellent invertebrate eyes (as in some cephalopod molluscs) have employed this force in the same way. In others, such as the compound

eyes first evolved by the crustaceans, the trick was never hit upon. Such eyes being solid, there is no possibility of rapid, gross, internal movements for accommodation, regulation of incoming light, and so forth. The vertebrate eye at the very outset received a tremendous boost toward its eventual superiority, when it luckily developed a vesicular plan of organization.

Origin of Intra-Ocular Fluids—In the eyes of the higher vertebrates, we can put our finger upon the immediate source of the internal fluid. It is certainly the ciliary epithelium, covering the ciliary folds and processes (Fig. 3, p. 7). But in the lowest vertebrates we see no such secretory structures, and a fertile field awaits the investigator of the sources of their aqueous humors.

Comparative physiology indicates that until there was need of an intra-ocular secretory epithelium, there was no ciliary body. And, until there was a ciliary body there could be no ligamentary anchorage of the lens, and no lens-squeezing methods of accommodation. We do not know for certain that the modern fish eye gets its water by osmosis through the cornea; but in the absence of any experimental work on this whole question, the assumption of such a process would explain much of the anatomical simplicity of the piscine anterior segment. The absence, from fish eyes, of those structures which terrestrial eyes have had to produce or have found it possible to produce, in consequence of their removal from water, is not adaptation to environment—unless one extends the term to include refraining from producing anything which is not needed. But these simplicities of the fish eye and complexities of the terrestrial eye are certainly related to environmental differences, rather than primarily to taxonomic ones.

All lampreys begin their lives in fresh water, and thus have the opportunity to fill their eyeballs by osmosis via the cornea, maintaining the desired intra-ocular pressure by controlled drainage through the ocular blood vessels. The several large, parasitic species which make their way to the sea must surrender any such ability unless they are able to raise the osmotic pressure of their intra-ocular fluids by excreting salts, glucose, or other substances into them. Failing this, they must somehow be able to secrete more fluid inside the eye from some of its tissues, even though we can see no special anatomical provision for such secretion. Moreover, since the marine lampreys are anadromous, they must shut off these compensatory intra-ocular secretions when they return to fresh water at the end of their lives to breed.

It would seem that there must also be a difference in the source of the water of the humors in fresh- and salt-water teleosts. The former are known to admit water readily everywhere through the skin, and to produce large volumes of urine in consequence. The marine teleosts, deprived of this use of osmosis, must fight for their internal water. They swallow sea-water and absorb it from within, excreting the excess salts by means of special cells in the gills.

No consistent differences have been reported between the eyes of freshwater and marine teleosts. If in the former the intra-ocular fluid and its pressure are recruited by osmosis through the cornea, it becomes a mystery where these come from in the marine form. If the latter gives off aqueous from the iris, falciform process, or hyaloid vessels, does this occur—and if not, what prevents it—in the freshwater eye? And, there are both anadromous (*e.g.*, the Pacific salmon) and catadromous (*e.g.*, the common eel) teleosts, whose eyes appear the same as regards possible secretory structures whether they are in fresh water or salt.

The elasmobranchs are mostly strictly marine though some, like the sawfish (*Pristis*) may enter perfectly fresh water; and several species are landlocked. All are known to maintain a high level of urea (2%) in their blood to give it a slightly higher osmotic pressure than the sea-water, so that they have as easy a time to maintain their general water balance as does the freshwater teleost; and like the latter they do not need to drink. They form little urine except when in fresh water, when they produce 50-100 times as much. In *Squalus,* at least, the intra-ocular fluids have been found to have a still higher osmotic pressure than that of the blood. It is therefore easy to believe that the intra-ocular water can come in through the cornea and that the intra-ocular pressure can be automatically regulated by controlled osmotic pressure; but it is a disturbing fact that the elasmobranchs are the only fishes which have ciliary folds (Fig. 104, p. 259). This makes it look, at first glance, as if they secreted their aqueous just as a land animal must. The ciliary folds are low and no more heavily vascularized than epithelial folds generally are, however, and moreover are blanketed (except where they continue, even lower, onto the iris) by the thick peripheral rim of the gelatinous 'zonule'. They do not appear to be advantageously organized for secretory purposes. Is their function purely mechanical, to increase the surface of attachment of the zonule? Franz believes so, since he found them best developed in the species with the most powerful lens-muscles. Are they even absorptive, the cornea being unable to control the amount of incoming water,

and letting through an excess as compared with that of a freshwater teleost? No experiments have been made to test this interesting possibility.

Effects of Water upon Light—Some other properties of water, salt or fresh, which affect aquatic vision *per se* regardless of the interspecific variation of fishes in their general make-up, are those which alter the amount and kind of light passing into and through it. To a vastly greater extent than in air, horizontal distances and vertical distances through water are not optically equivalent. As sunlight penetrates downward into water, it undergoes extinction, which is a blanket term embracing both absorption and scattering. Off Plymouth, England, 90% of white light was found to be extinguished at eight or nine meters, 99% at 35 meters. These effects vary from one body of fresh water, or part of the sea, to another and there is no close agreement between investigators as to what is normal or average. Roughly however, a depth of 535 meters in the clearest waters is characterized by utter darkness as far as human vision is concerned. Beebe found only a 'bluish glow' at 435 meters off Nonsuch Island. Some seas are completely dark at 200 meters, dirty harbors in a few meters. Even the clear Bermudian seas seemed to Beebe the 'blackest spot on earth' at a depth of half-a-mile.

The various wavelengths of light do not all reach to the same depth. The ultra-violet is almost all eliminated in a few millimeters of water, though *traces* reach to greater depths than any other wavelengths—enough, at 1000 meters, to affect a photographic plate, though only after 80 minutes exposure! The infra-red (heat) rays are cut out in a few centimeters, or a meter or so. As the light descends, the ends of the spectrum are pared off, the long-wave end more rapidly (90% of the red is gone at five meters), until a band is left whose wavelengths continue to penetrate about equally well. The limits of this band, as determined by a photographic technique, are from λ510mμ to λ540mμ. Beebe, in the bathysphere, reported that at 250 meters all that was left of the spectrum was a narrow band centering at λ520mμ. This visual observation checks well enough with the results obtained by lowering remote-control cameras to various depths. Not that there is much of this light—90% of the green part of sunlight is already extinguished at thirteen meters.

It is more than a coincidence that these best-penetrating wavelengths should be identical with those to which fish rhodopsins are most sensitive. The rhodopsins of land animals have their absorption maxima averaging at around λ500mμ (that of the ox, for example, is λ495mμ—of man, about λ500mμ); but it must be remembered that the first rhodopsin was

invented by pro-fishes, and partly for the purpose of allowing them to go down from the surface to the less brightly lighted depths. A group of English workers recently found that the absorption maxima of a number of marine fish rhodopsins range from λ505mμ to λ545mμ. They hoped to find a relation between the particular maximum of a given species and the depth preferred by that species. This was not established; but the investigators failed to take the broader viewpoint, from which one can see that since the λ510-540mμ band penetrates deepest, it will be most conspicuous in the spectrum at any lesser depth. And since the sun's rays within this range have equal facility of penetration through water, a rhodopsin would be maximally efficient with its absorption peak located anywhere in this band.

There *may* be a close adjustment of a particular fish to a particular quality of light available at his preferred depth—it may be that the investigators mentioned were simply unable to obtain sufficiently accurate information as to just what depth a given species does prefer. More probably however there is a weight of other factors which usually make it impossible for a fish to be at all precise in this matter. A sandy-bottom species like a flounder, for instance, has to be content with bottoms which vary considerably in distance from the surface. Even more upsetting are the barrier-effect of the thermocline and the seasonal turnover of lakes, for a fish which responds to critical temperatures may swim at one depth for a part of the year and at a very different depth, or at no particular depth, for another period. Still other fishes may be free of any control by the thermocline and still show no close restrictions as to depth. The wall-eyed pike, for example, remains in deep water by day and comes into the shallows to feed at night. Many marine fishes also show such rhythms. *Astronesthes,* for example, lives in the gloom at 200 meters by day and follows the twilight upward to spend the night at the surface. Such fishes are responding to a particular *quantity* of light regardless of the time of day, or the depth, at which they find it, and not to a *quality* of light which is characteristic of a particular depth when the sun is high.

Since we are thus led to expect only a very general correspondence between differential sensitivity and depth of swimming, the λ505-545mμ range of rhodopsin maxima seems close enough to the λ510-540mμ band of best-penetrating wavelengths to give us the right to say that the very color of rhodopsin itself, like the ruddy color of some photosynthetic pigments of the deepest-living seaweeds (Rhodophyceæ) is an adaptation to water. That same red color, in human rhodopsin, is still another heritage

from our immensely remote aquatic ancestors. If rhodopsin had been first invented on land, it might very well have been purple, not red.

In some freshwater and anadromous fishes it has recently been found that the absorption maximum is roughly intermediate between those of marine fishes and land animals, the value being $\lambda 522 \pm 2m\mu$. The investigator (Wald) has called the photosensitive substance involved 'porphyropsin'; but there is little excuse for the new word. Rhodopsins have been re-invented so many times that if we coined a new name for each one that we can distinguish chemically or spectroscopically, the nomenclature would soon be hopelessly confused. There is even good reason to think that in marine fishes there are *two* rhodopsins simultaneously present, the effective absorption maximum of the rods being dependent upon the relative amounts of the two.

An important effect of depth upon light-quality is happily significant for every fish. This is the rapid extinction of ultra-violet. In this part of the spectrum there is one band of wavelengths, from $295m\mu$ to $305m\mu$, which is particularly harmful—positively lethal, in fact—to living tissues. This is consequently known as the 'abiotic' range. No aquatic species need concern itself with protection from abiotic light; for even if the water were chemically pure, a few millimeters would absorb it all. The dissolved and suspended matter of natural water disposes of it even more promptly, by fluorescing it into harmless visible light. Land vertebrates, diurnal ones at any rate, have had to evolve a capacity for fluorescence by their lenses. Aquatic forms frequently show no such capacity, for they do not need it. Stickleback and toad lenses are very transparent to ultra-violet, frog and carp lenses less so.

More important than the qualitative effects of water upon light are its quantitative ones. Even if extinction with depth were not selective, it would still affect aquatic vision profoundly—as is emphasized by the visual problems of the deep-sea fish, shortly to be considered. Even close to the surface, vision in the horizontal direction is greatly dimmed. To put the matter crudely, we cannot see the side of a light-beam—only its end, and for light to enter the eye it must be sent or reflected directly toward the organ. Under water, there are not nearly as many reflecting objects in the plane of the eye of a fish—particularly in the open sea—as there would be on land. Such light as *is* aimed at the eye is weaker because there are few hard and smooth, hence brightly reflective, surfaces; and this weak light is further weakened through scattering by suspended matter. All in all, if a fish or whale can distinguish objects fifty feet

away at his own level, it is a red-letter day for him. With increasing depth, or increased turbidity, this distance is still further reduced since the absolute amount of light reflected into the eye of the animal depends upon the relative amount of sunlight reaching that depth.

Under water, vision is handicapped while other senses are actually promoted. It is not surprising that the fishes are better able to get along, if blinded, than any other vertebrates. They use their eyes when they can, but most fish can find enough to eat without seeing the food. Many fishes are deprived of vision in winter, when the ice above them is blanketed with snow, and some arctic species live out their whole existence under

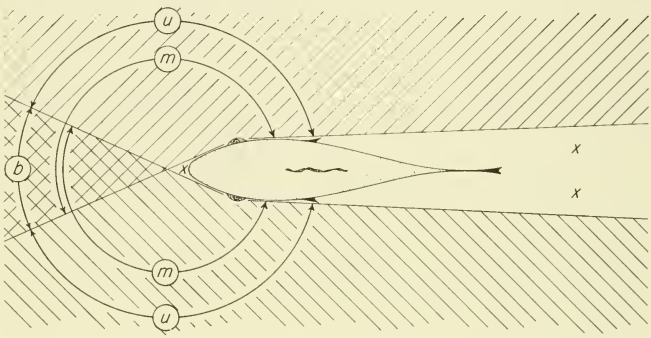

Fig. 128—Fish from above, showing visual angles in the horizontal plane.

This particular fish does not have complete periscopy—with a less bulky body the posterior blind angle would diminish; but the anterior binocular field might then also be reduced. *b*- binocular field; *m, m*- monocular fields; *u, u*- residual, uniocular fields; *x, x*- anterior and posterior blind areas.

such conditions. No wonder, then, that so many fishes have been able to establish themselves and survive in lightless caves.

The optical density of water has interesting consequences upon aquatic vision, particularly upward through the surface and into the air. Repeated allusion has already been made to the fact that the corneal tissue has about the same refractive index as water, so that the cornea is in effect optically absent under water, and the first bending of incoming light-rays takes place at the surface of the lens. This requires the lens to bulge far through the pupil if that aperture is not to limit greatly the visual field (Fig. 105b, p. 261); and the lens must project from the sur-

face of the body itself if periscopy—180° vision for either eye, 360° vision for the two together—is to be attained in a fish whose eyes are back to back (Fig. 128). To many a swift form—the tuna, for example—streamlining is more important than periscopy, and the eye is not allowed to protrude. The broad cornea of a fish eye is not at all related to light-gathering power as it would be in a land animal—the relative size of the pupil, by itself, determines the brilliancy of the retinal illumination (see p. 211).

The importance of periscopy to a fish is not only seen ecologically, in his increased awareness of near-by prey and increased difficulty of approach by enemies, but is also seen anatomically in his lack of a neck. Despite his buoyancy and rotability on his vertical axis, a fish would need a neck almost as badly as a land animal, were it not for his full visual field. Periscopy has not been important to whales, because vision itself is unimportant to them; but the seals have retained it by keeping the neck flexible—which the whales and sea-cows have not done.

Looking Through the Surface—When the surface is almost literally as still as glass, an underwater animal can look up through it, but with such peculiar consequences that they may account for the bewildered expression of the average fish! A light ray passing through a rarer medium and striking a denser one will enter the latter from any angle of incidence; but for rays passing from denser media into rarer ones, there is a 'critical angle' of incidence at which they are bent just enough to skim the boundary surface. At greater angles, they are totally reflected and cannot escape into the rarer medium at all. With light, there obtains just the inverse of the situation when a gun is fired at a submerged submarine—if the boat is too far away and the angle of fire too flat, the shell cannot enter the water, and reflects, *i. e.* ricochets, harmlessly from the surface.

The consequence of this is that if a fish looks slantingly upward at the surface, he cannot see through it, but instead sees mirrored upon it objects which are on the bottom at a distance (Fig. 129). If he looks more directly upward, he sees into the air. In effect, there is a circular window in the surface through which he can look (Fig. 129a). This window enlarges if he sinks, shrinks if he rises, but always subtends an angle of 97.6° (in fresh water) at his eyes. If the bottom is distant, the surface outside the window is silvery with the reflection of the light scattered in the water, and this light of course always washes over and dilutes the

image of the bottom, even when the latter is close enough to the surface to be seen reflected from it.

Through his surface window the fish sees everything from zenith to horizon in all directions. This hemispherical aërial field is not narrowed

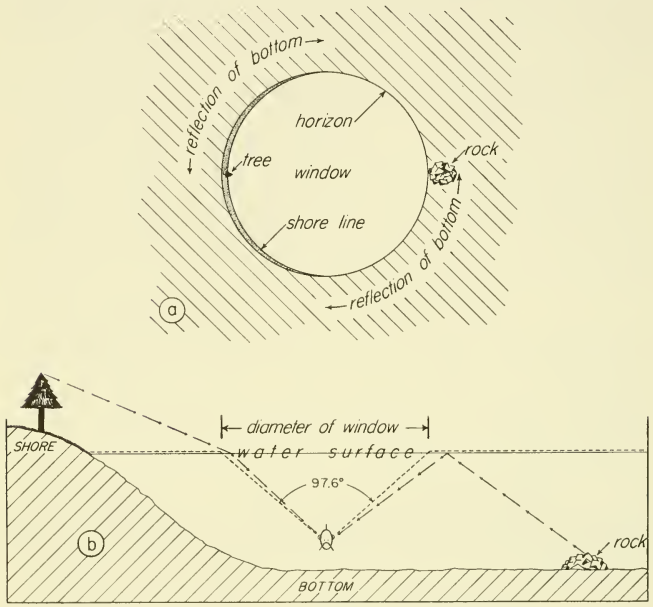

Fig. 129—Visual field of a fish in the upward direction.

a, the water surface and the aërial window as seen from beneath. b, explanation of the window: rays striking the surface at an angle within the window are refracted to the eyes of the fish, but rays striking outside the window from beneath are totally reflected. Within an angle of 97.6° the fish sees out into an aërial hemisphere; but outside of this angle he sees objects on the bottom, reflected in a silvery surface. The surface must of course be completely calm.

or widened according to the size of the window and the depth of the fish. It always contains everything above the plane tangent to the water surface at the rim of the window, but the distortion and the brightness of objects within it do vary. The objects seen proportionately largest are

those directly overhead. If an object should swing down a semicircle from the zenith toward the horizon, along a meridian of the aërial hemisphere, it would get shorter and shorter in its meridional length and in its width measured parallel to the surface. Thus even though its linear distance from the fish were constant, its apparent size would become smaller, the closer it approached the horizon. It would be seen more and more dimly, too, for light rays which make small angles with the water are largely reflected, and but little of such light is refracted down through the surface to enter the eye of a fish.

The entire circumference of the 'horizon', which a swimming man could see by treading water and rotating 360° on his axis, is, for the fish, contracted to the few inches or feet of circumference of his surface window. It follows that a man standing on the bank of a pool is seen as a tiny doll by a fish which is a few yards away and only a few inches below the surface. Our tendency is to suppose that the fish will see us more poorly still, just as we see *him* less well, if he drops deeper in the water; but since dropping lower enlarges his window, it magnifies objects on the shore—magnifies them, that is, as compared with their apparent size when the window is smaller. To see the fisherman optimally, then, the fish must seek a depth from which the improvement of visibility through enlargement is not cancelled by the loss of light through the greater distance of water through which the rays must travel to his eyes. The poor fish is thus fated never to see us as we are—even through the flat glass side of an aquarium tank.

Streamlining of the Eyeball—Except in placid, slow-swimming species, the fish eye must ordinarily bear some structural adaptations to its propulsion through the water. The considerable resistance of the medium has two effects upon the eye of a fast-moving fish: friction, tending to scour and erode the corneal epithelium; and asymmetrical pressure. To combat these effects the eye, like the body as a whole, must be streamlined. The ocular streamlining is of some importance in reducing general bodily water-resistance; for the contribution of the eye, though it may bulge only a bit from the head, is not negligible. The streamlining of the eye affects the eye itself, and helps substantially to maintain the optical *status quo*: the moving cornea receives added pressure on its advancing nasal border, and at the caudad border of the exposed part of the globe a region of lowered pressure exists as on the upper surface of an airplane wing. These differential pressures would lead to a distortion

of the eyeball, and to a disturbance of its optical performance, if they were not somehow minimized.

The reduction of friction and of the asymmetry of pressure is partly effected by the ellipsoidality of the eyeball. The visual axis of the fish eyeball, as we have seen, is almost always its shortest diameter. Its horizontal, cephalo-caudal diameter is commonly its greatest dimension, and may exceed the vertical diameter by fifty per cent or more (Fig. 104, p. 259). Thus the pelagic fish eye, partly for the sake of streamlining and partly for the sake of a wide horizontal visual angle—which swift fishes of course desire—is not a ball, but is rather an 'ellipsoid of revolution'. It presents to the water a portion which, as to curvature, is shaped like the

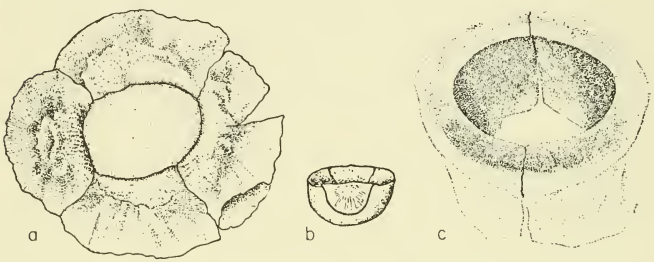

Fig. 130—Scleral ossicles in fishes. After Edinger.

a, an arthrodire, *Dinichthys gouldii*, exemplifying the four-part ring characteristic of many ancient fishes. × ½ b, pike, *Esox lucius*; scleral cartilage and the two ossicles characteristic of modern teleosts. × 1. c, tuna, *Thunnus thynnus*, showing return to complete ring (which, however, involves but two ossicles). × ½.

bowl of a teaspoon; and, of course, the part of the eyeball which shows through the lid-opening can still be, and often is, quite circular in outline—just as we can easily cut a circular piece out of a teaspoon. Past the teaspoon-surface, which is often a part of the head-surface itself, the water may stream with the least possible distortive action. The cornea may be rendered violently astigmatic by its dual curvature (see Fig. 13, p. 28), but since its surface is under water, no optical harm is done. The spherical lens, alone, is forming the image on the retina.

In lampreys the ellipsoidality or horizontal elongation of the eyeball is very slight, but the eye is smoothly covered by the primary spectacle anyway (see section D). Ellipsoidality is very marked in many elasmobranchs, which are often swift swimmers as their predatory habits natur-

ally require them to be. The cornea is not flat as in teleosts, since the elasmobranch lens must have room to move forward in accommodation; and the outline of the cornea is often involved in the ellipticity, being then much broader than it is tall. Practically never—*Lamna* is an exception—is the vertical diameter of the cornea at all greater than the horizontal. The cornea is thin centrally, and markedly thickened toward its rim (Fig. 104), a construction which makes of it a more sturdy dome than it would be if it were uniformly thick, and also leaves more room for the lens to increase its distance from the retina. Among the chondrosteans and holosteans, the shark-like sturgeons and the gars (which make swift dashes after their prey) have ellipsoidal eyeballs. Not so the slow-swimming *Amia*.

In the teleosts a pronounced bulbar ellipsoidality is common, and the cornea is often more or less oblong horizontally as well. Characteristically, the piscine sclera consists largely of a cartilaginous cup, which is often calcified (and, in *Tetragonopterus*, is entirely bony). In many teleosts, additional support for the anterior part of the sclera is afforded by a pair of osseous demilunes, disposed nasally and temporally around the cornea (Fig. 130b), and sometimes fused above and below into a continuous ring. These demilunar ossicles are embedded in the connective tissue of the sclera, and are best developed in the swiftest swimmers. They are heaviest of all in the tuna (*Thunnus*) and the swordfish (*Xiphias*), where they form a complete, deep 'napkin-ring' enclosing nearly the whole of the eyeball (Fig. 130c). These ossicles have nothing to do with the imbricated scleral ossicles of the Sauropsida (see p. 271), which are homologous with the circumorbital bones of fishes. The demilunes of modern teleosts probably represent the anterior and posterior members of a quartet of ossicles which, in some of the oldest of fossil fishes, formed a complete circumcorneal ring (Fig. 130a).

'Adipose Lids'—In addition to the streamlining effect of an ellipsoidal cornea, supported by scleral ossicles, many swift teleosts possess so-called adipose lids, whose effect is to cover the circumocular sulcus and thus eliminate distortive eddies in the slipstream alongside the eyes (Figs. 131a and 132).

Considering their usual orientation, these lids are better called *vertical* lids, for they are rarely truly adipose. *Mugil cephalus* forms an exception —here, the lids are usually puffy, and may contain so much lipid substance that they turn yellow and opaque in preserved specimens. Ordinarily the vertical lids are very thin, and are perfectly transparent where

they overlap the cornea. They consist of basophilic mucous, muco-areolar, or sometimes fibrous or cartiloid connective tissue. In some forms, as *Scomber,* they are said to become thickened and charged with fat during the breeding season. In some species (salmonoids, particularly) they have been described as anchored to orbital bones by special ligaments, or to be movable by special muscles; but these points are in dispute.

In various pelagic teleosts, the vertical lids present themselves in essentially three conditions. Typically, they consist of a pair of ingrowths (minus an epidermis) of the skin which, in fishes generally, forms the outer lip of the circumocular sulcus (Fig. 151b, *m*; p. 451)—the line of

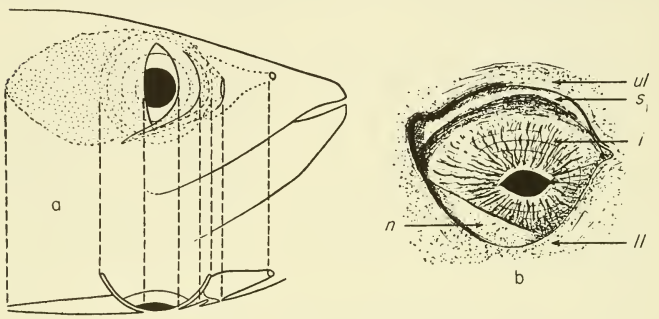

Fig. 131—Permanent lid-complexes in fishes.

a, head of a teleost, *Scomber scrombrus,* showing vertical ('adipose') lids in surface view and in section. After Hein. b, left eye of a requin shark, *Galeorhinus galeus.* After Franz. *i*- iris; *ll*- lower lid; *n*- 'nictitating membrane'; *s*- sclera; *ul*- upper lid.

junction between the conjunctiva and the surface skin of the head. More often than not, the anterior fold smoothly joins the posterior one above the eye, but overlaps the posterior fold inferiorly (Fig. 132b, c, d, f).

A series of species could be selected in which, by imperceptible steps, this situation would intergrade with one in which the cornea is surrounded and overlapped by a practically circular, continuous fold, of about the same width in all meridians (Fig. 132g). Various conditions in this series may occur in the same genus, as in *Mugil, Caranx, Scomber,* and others. The anterior and posterior lids may be equally developed, or —much more commonly—the posterior may be the wider of the two. Very rarely (*e.g.,* in *Mugil bleekerii*) the anterior is the broader. The

aperture between well-developed lids is a narrow vertical ellipse (Fig. 132d), but tends toward a large circle as the lids are reduced in extent. Where the lids are narrow, they are usually continuous inferiorly as well as superiorly, instead of being overlapped (Fig. 132e, g). There are instances in which a given genus has prominent vertical lids, while a related one with closely similar habits is without them, perhaps owing to total disappearance. *Tarpon* for example has no lids, whereas the ten-pounders (*Elops*) have them well developed.

Lids of the types just described are especially characteristic of the herrings and their allies, constituting the 'clupeoids', among the soft-rayed teleosts (Malacopterygii). They have been independently evolved

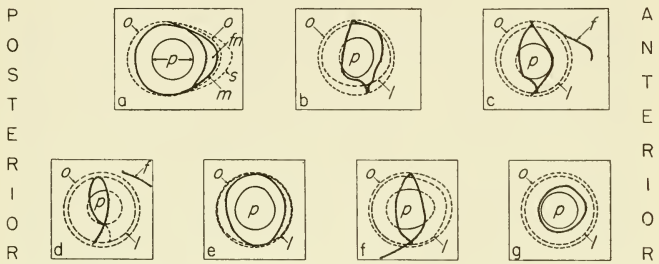

Fig. 132—'Adipose' lids in various teleost fishes (drawn from preserved specimens).

a, *Salmo gairdnerii irideus.* b, *Clupea harengus.* c, *Nematalosa nasus.* d, *Pomolobus chrysochloris.* e, *Hiodon tergisus.* f, *Rastrelliger loo.* g, *Mugil cephalus.*

f- fold or ridge in head skin; *fn*- 'false nictitating membrane'; *l*- limbus corneæ; *m*- margin of circumocular sulcus; *o*- wall of orbit; *p*- pupil; *s*- extremity of recess under *m*.

also by equally swift, pelagic members of the more advanced spiny-rayed division (Acanthopterygii). The correspondence between *Pomolobus* (Fig. 132d), a clupeoid, and *Rastrelliger* (Fig. 132f), a scombroid, is quite perfect. *Mugil cephalus,* another acanthopterygian (Fig. 132g), has its counterpart in the clupeoids *Amphiodon* and *Hiodon* (Fig. 132e). Among both malacopterygians and acanthopterygians there are families in which the aperture between the vertical lids has been quite obliterated, so that there is an unbroken covering over the eye. Though this is of course also a streamlining adaptation, and probably an even better one than the separate, apertured lids, it is discussed later in connection with the other types of 'spectacles' to which it is morphologically related.

The salmonoids (salmons, trouts, whitefishes) present a condition which differs considerably from both the two-lids-overlapped and continuous-circular-fold extremes, and from any situation intermediate between them. The salmonoid complex (Fig. 132a) consists of a narrow, crescentic posterior lid running around two-thirds of the circumference of the eye (and comparable with the posterior lid of a herring or a mackerel) together with a broad, roughly triangular, anterior fold. The latter is depressed below the surface of the head, for it is developed not from the extreme margin of the circumocular sulcus, but as a separate conjunctival fold arising from beneath that margin, on the anterior side of the membranous orbit.

It is hard to say whether this arrangement has been derived from one like that of the clupeoids, or is quite independent. Ecologically, it probably has a special significance. The eye is not actually as well streamlined as it would be if the anterior sulcal margin were to recede smoothly into the head surface, thereby creating something more like the arrangement in *Hiodon*. In the salmonoids, the bony orbit is incomplete anteriorly, and it may well be that they have taken the opportunity to draw the anterior sulcal margin well forward, primarily to permit of more straightforward vision and a wider binocular visual field during the pursuit of prey. The broad, stiff, anterior lid-fold of the salmonoids, which has been called a 'false nictitating membrane' (Fig. 132a, *fn*), can thus be thought of as having been left behind by the forward-migrating sulcal margin (to prevent the opening up of a gap between the latter and the cornea), rather than as having grown actively, posteriorly, toward the center of the cornea as the anterior lids of the clupeoids and scombroids have certainly done.

Bottom Fishes—A host of coastal fishes, both elasmobranchs and teleosts, have chosen to live on the bottom. By thus putting their backs against a wall and living at the center of a hemisphere of space rather than a sphere, they have halved the job of watching out for enemies and prey. At the same time they are close as can be to a retreat or a camouflage—in crevices or burrows, or in the sand or mud with which they can cover themselves. Living as they do in such intimate contact with their chief food supply, the other members of the 'benthos' or bottom fauna, many crevice- and mud-dwelling fishes have found vision of little use, and have allowed their eyes to become small or degenerate—or even to dwindle to tiny, blind remnants under an opaque skin (Fig. 133b, p. 387).

Other fishes have become adapted to live on, rather than in, the substrate, most of these being dependent for concealment upon their inconspicuous shapes and colorations. The bottom elasmobranchs—the skates and rays, the sawfish (*Pristis*), the guitar-fish (*Rhinobatos*), and the ray-like shark *Squatina*—have a depressed form. A consequence of their dorsoventral flattening has been an equal rotation of their two eyes so that they look more or less upward—in *Squatina,* for example, the visual lines slant upward at 45° angles. A number of teleosts have evolved the depressed shape also, the angler-fish *Lophius* for example, and to a less degree the stargazers (Uranoscopidæ); but most flat-lying teleosts are among the more than 500 species of the flatfish group:

In the flatfishes, the laterally-compressed animal has simply lain down on its side (right or left, according to species) during its individual development. The new under surface remains unpigmented and loses its eye, by migration over the top of the head (or even through it), to the new upper or eyed side. In the more specialized flatfishes the mouth tries its best to twist too, but not very successfully, so that it works largely crosswise. The beginnings of the flatfish habit can be seen in some sea-perches which habitually rest on their sides, the families Serranidæ and Labridæ particularly. In one primitive tropical flounder (*Psettodes erumei*), the eye from the future blind side stops at the crest of the head, never moving completely over onto the eyed side to join its non-migratory fellow. Unlike other flounders, individual *Psettodes* may end up lying on either the right side or the left—that is, either eye may be elected to migrate. The dorsal fin commences behind the head in this species, whereas in a perfected flatfish it waits until the migration of the eye has taken place, and then grows forward—cutting off the eye's retreat, so to say.

A topside position and approximation of the eyes brings with it an advantage and a disadvantage, to either or both of which various fishes have responded adaptively. The advantage is the opportunity to secure an exceptionally broad binocular visual field, especially in an upward direction, with a consequent improvement of space-perception. The disadvantage is that the eyes are subjected to dazzlement by the vertically incident sunlight.

Some upward-looking bottom fishes have met the problem of dazzlement by placing the eyes so that they can look horizontally, permanently. The dorsal binocular field may then be largely sacrificed, of course, as in *Manta.* Others, such as *Lophius,* are able to swing the eye downward

until it aims horizontally, there being a special provision for this in the form of a temporary lower lid. Still others have kept the eyes aimed more nearly upward and have given them protection, from over-stimulation, by means of expansible pupillary opercula.

Such an operculum is most nearly a group-character in the batoids (*i e.,* rays in the broad sense). These elasmobranchs (but not *Squatina*) lack the eyelids (Fig. 131b, p. 382) which characterize the bottom-loving sharks (*Galeorhinidæ*), but they can nevertheless retract and 'close' their eyes at times to shield them from strong light (p. 452). The eyes are relatively small, as they are in all upward-lookers, which have not the need for a large pupil that a lateral-eyed fish has. A ray's eyes are little more than half the size of those of a shark of equal size. The pupillary operculum ordinarily has a smooth margin (*e.g., Torpedo, Trygon, Myliobatis*), but in Raja it is serrated so that, on full expansion, it reduces the pupil to a crescentic series of stenopaic apertures (Fig. 65b, p. 158). The operculum of *Torpedo* is small, but it can cut the slender, horizontally oblong pupil quite in two. In the mantas or devil-fishes (Mobulidæ) and eagle-rays (Myliobatidæ), the eyes aim not upward but laterally, due to the presence between them of a pronounced ridge of head material. The mantas lack a pupillary operculum, though one is present in *Myliobatis*.

A mutual exclusiveness of pupillary opercula and turreted orbits is also suggested by the situation in teleosts. The operculum varies from small (in the star-gazer, *Uranoscopus scaber*, where it is dentate—see Fig. 65d) to large (flounders), and is remarkably developed in the armored catfish *Plecostomus* (Fig. 65e, f, g). The bulk of the flounders are included in the families Bothidæ (left-handed) and Pleuronectidæ (right-handed flounders). In the bothids, the eyes tend to lie fairly flat in the head, and an operculum (Fig. 65c) is the rule; but the eyes of pleuronectids, by and large, lack opercula and can be elevated hydraulically, and swivelled about in the horizontal plane by a special slip of the superior oblique muscle. Some pleuronectids, however (*e.g., Platichthys flesus*), do have opercula. The ocular turrets of flatfishes make it possible for them to see even while the body is sifted over with sand for concealment. A lateral aim of the eyes obviates any handicapping of the horizontal vision of the animal when it rises from the bottom to become pelagic for the nonce, as do the mantas, eagle-rays, and many flatfishes. The binocular vision, now forward, now upward, of the turret-eyed flounders gives these fishes what has been called an 'intelligent' look.

While the eyes of most good-eyed bottom fishes look perpetually upward, those of one genus, *Corydoras,* periodically look sharply downward. These are tiny South American armored catfishes which are popular as scavengers in home aquaria, and they are commonly believed to be 'the only fish that wink'. Since there are no lids, there is no true wink—the eyeball simply rolls downward until the pupil is largely or wholly concealed; and the gray superior conjunctiva, which is thus exposed, does give the appearance, from above, of an upper lid going into action. The utility of this phenomenon is not apparent. It might be suspected that the fish has an upwardly-aimed fovea, and has to turn the eye down to use the fovea for occasional horizontal vision; but serial sections of a *Corydoras* eyeball have revealed no such feature.

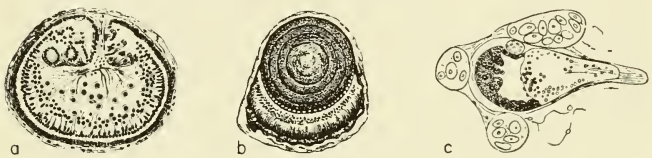

Fig. 133—Microscopic, degenerate eyes of blind fishes. After Franz.

a, a hagfish, *Myxine glutinosa* (internal parasite). b, a goby, *Trypauchen wakæ* (littoral, crevice-dwelling). c, an amblyopsid, *Troglichthys rosæ* (cave-dwelling).

Cave Fishes—The cave fishes come close to bowing themselves entirely out of this book, for most of them have 'no eyes worth mentioning' (see Fig. 133c). The origin of the cave habit, and the cause of the disappearance of the eyes, are fascinating puzzles however. Cave fishes belong to many different families and represent many independent invasions of the cave habitat. All are members of teleostean families in which normal-eyed fishes occur, though the eyes of these 'outside' relatives are sometimes very small. The North American group of cave forms (the family Amblyopsidæ) have but one non-cavernicolous representative, and the eyes of this form (*Chologaster*, in the Dismal Swamp) are much reduced.

Only a very few cave species—notably, several catfishes of the genus *Rhamdia*—have kept their eyes in good condition. One, the Mexican *Anoptichthys jordani,* was lately shown to contain normal-eyed individuals as well as others showing all grades of reduction of the eye, down to obsolescence. Such forms have perhaps not long been in the cave environment. But, with the possible exception of *Anoptichthys,* no known

cave fishes are believed to have become such through entering caves as 'strays'. On the contrary, much of the evidence suggests that the species which have taken up residence in caves have ordinarily been well prepared in advance to get along in lightless surroundings:

Many fishes which live in rocky crevices, on muddy bottoms, or in silty rivers and estuaries, have greatly reduced eyes. Some are even blind, with a microscopic and sadly imperfect eyeball covered with opaque skin or embedded deep in the tissues of the head. In such dim-light fishes, as in many deep-sea forms, the other sense-organs are especially developed, notably those of the tactual and chemical senses. The animals are thus well fitted to find food where it is scarce as well as invisible. The ancestry of most cave fishes can be traced to such forms. It appears that the typical cave species is one which has taken naturally to the cave and has welcomed the refuge it offered—not one which has wandered in accidentally and been unable to get out again. Stray individuals of normal-eyed species are encountered in caves, but many of these belong to groups living outside whose way of life, and sensory and reproductive equipment, would not seem to make them good recruits for the permanent cave fauna.

Tiny-eyed, nocturnal, bottom-grubbing catfishes of several families have contributed more cave species than any category of outsiders. No cavernicolous gobies are known, but ichthyologists would not be surprised to discover one at any moment, for many of the 'sleepers' live on muddy bottoms or in crevices, and have degenerate or obsolete eyes (Fig. 133b). One intertidal species, *Typhlogobius californiensis,* shares its rocky hideaway with a blind species of shrimp—a pair of the blind fishes and a pair of shrimps inhabiting each burrow. When adult, the fish is quite dependent for food upon the activities of the shrimp—almost a case of the blind leading the blind!

Some especially interesting contributions to the cave fauna have been made by the family Brotulidæ. The brotulids are essentially a deep-sea group. Some species (a couple of them, blind) have secondarily come to the surface to live on reefs. Still others have made the doubly remarkable transition to fresh water and the cave habitat—*Stygicola* and *Lucifuga* in Cuba, and another (*Typhlias*) recently discovered in one of the caves of Yucatan. In the brotulids, the amblyopsids, various families of catfishes, and still others, we see clear indications that what has been called 'pre-adaptation' to relative lightlessness can lead to the easy adoption of the cave habitat. And probably such pre-adaptation is practically indispensable, if the invasion of the cave is to be successful.

Just how the eyes of any blind fish species were led to disappear, we cannot say. An old idea was that where the eye had become useless, there was a positive incentive for eliminating the organ, since this would save energy both in adulthood and—especially—during growth. This notion seems ridiculous nowadays, for the proportion of a growing animal's food-intake which goes to enlarge the eye is negligible. Most of the energy released from food goes for motor and secretory activity, and only a very small part of the food is converted into new protoplasm. Nor does the disappearance of an eye leave a hole in the head—its volume is occupied by tissues (mainly muscle) which consume just as much energy as the eye had done.

Though a normal eye is excess baggage to a cavernicolous or limicolous fish, there appears to be no urgent reason why he should get rid of it. Useless organs do not always promptly disappear simply because they have become useless—as witness the human appendix, coccyx, platysma, tonsils, wisdom teeth, *et al.* We are left to suppose that in the immediate outside ancestors of most cave species the eye was 'trying' to disappear anyway, but was prevented from doing so, by natural selection, because it was useful and necessary. The usefulness once removed by the assumption of cavernicolous life, the inherent tendency for the eye to shrink was allowed to express itself, even unto the logical end-result—complete loss.

This explanation does not tax the imagination of ichthyologists as severely as one might think. In many an open-water fish species, reduced-eyed individuals appear as soon as the food supply is made abundant and predatory enemies are removed. Lack of competition then permits the full development of individuals which, since their germ-plasm has undergone 'mutations of loss', would formerly have been suppressed by starvation or capture. Loss-mutations are known particularly to affect the more complex organs of vertebrates, such as the eye. A species or family in which such mutations occur with especial frequency has of course no advantage, over others, in any attempt to become adjusted to a habitat in which the illumination is reduced or absent. But if a group which throws loss-mutations also produces an unusual number of other trial-and-error modifications (as seems likely), then such a group might readily evolve the dermal sense-organs, barbels, or whatnot required to cope with a dim-light environment. Once adapted to dim-light existence, such a group would actually be better off in a cave, if it happened to find one, than outside where there were predators to be dodged. And once inside the cave for good, a rapidly-mutating species would inevit-

ably lose what remained of its eyes, though without being under any positive necessity of doing so. As to whether *Rhamdia* spp. have only just found their caves, or are simply slow mutators—the reader may take his choice.

It is perhaps worth pointing out that even an individual fish, of some kinds, may be unable to retain useful eyes if kept in darkness. Ogneff, thirty years ago, kept some goldfish in the dark for three years. At the end of that time they had lost their skin pigment, their eyes had degenerated greatly—though not in any close imitation of those of normally-blind fishes—and they were quite unresponsive to light. Conversely, it has been found that in cave salamanders (*Proteus, Typhlotriton*) whose larval eyes normally retrogress at metamorphosis to the point of obsolescence, the eyes can become quite normal salamander eyes if the larvæ grow to adulthood in the light. These sightless amphibians thus become blind in each new generation. No mandatory degeneration of the eyes is genetically fixed in the species—merely a capacity of the whole eye to retrogress if it is not used past a certain point in its development, as in the case of Ogneff's goldfish.

Whether or not the adult ocular degeneracy of any, or many, cave fishes has a similar basis, is something for future experiments to decide. And, the cave fishes are but one facet of the general problem of quasi-eyelessness. Blind, fossorial species are to be seen in every class of vertebrates except the birds.

Parasitic Fishes—One strange habitat, which is about as lightless as any, is the interior of an animal. The hordes of internally parasitic invertebrate animals are all eyeless, with the other sense-organs, as well as the organs of digestion and locomotion, greatly reduced or absent.

A very few vertebrates, all of them fishes, are parasitic. The larger lampreys are external parasites on other fishes. While clinging to a host, a lamprey has little need for vision; but since lampreys ordinarily consume only blood, they necessarily spend a good deal of time off of hosts, engaged in a search for the next victim. Their eyes are important at such times, for the exploration is largely visual—it has been shown that lampreys are attracted to any light-colored object (which could seem to them to be a fish's belly) moving through the water. They will cling to a white-bottomed boat, but not to a dark one; and lampreys have given considerable trouble to human swimmers by mistaking them for fishes. The eyes of lampreys (Fig. 103, p. 258) are excellent visual organs and are in no way degenerate.

The hagfishes, which are the other great division of the cyclostomes or marsipobranchs, are on the other hand completely blind, their eyes (Fig. 133a) microscopic and concealed. The hags are internal parasites of larger fishes—internal predators would perhaps be a better term. They are extremely voracious and eat everything of their victims except the skin and the skeleton. While inside a fish, a hag has no more need of eyes than a tapeworm. In contrast to lampreys, they spend less time away from a host since they give the latter so much more 'attention'. Moreover, hags are deep-water forms, with admirable tactual and chemo-sensory equipment for locating prey on the bottom by horizontal exploration. They are thus able to dispense with eyes entirely.

One teleost, *Simenchelys parasitica,* leads a quite hag-like existence. This entoparasitic eel is most commonly seen emerging from captured halibut, but it attacks many other large fishes. *Simenchelys* may prefer the lightless deep sea, for it has been taken at 2000 meters. The eye is covered by skin, which in life may be clouded or opaque; but the eyeball itself may be six millimeters in diameter, and might be called reduced, but scarcely degenerate.

Still another teleost, the pearl-fish *Encheliophis jordani,* may be regarded as an entoparasite or as an internal commensal, depending on one's point of view. This little fish spends much of its life inside the cloacæ of sea-cucumbers, but it does swim freely in the water at times. The pearl-fish offers an interesting parallel to *Rhamdia* and *Anoptichthys,* in that it gives indications of not having long lived in its currently favorite lightless habitat. The eyes are aimed dorsally, and their circular pupils are able to contract to mere dots. These features strongly suggest that *Encheliophis,* not so long ago, was a free living upward-looker with habits similar to those of the flatfishes.

Deep-Sea Fishes—After the teleosts crystallized out of the holostean stock (see Chapter 6), they gradually evolved into a large group in which a fundamental schism soon appeared. One great, primitive branch of the class, the Malacopterygii, is characterized by soft fin-rays. The most specialized division, the Acanthopterygii, derive their name from their spiny fin-rays. The spiny character has been lost secondarily in some families whose affinities are clearly with the acanthopterygians. Other families with soft rays, making up the assemblage called the Anacanthini, are sometimes classed with the malacopterygians and sometimes kept apart.

Carl Hubbs has pointed out that the acanthopterygians, by and large, are adapted for a shallow-water, shore existence. They have spread far and wide into fresh waters, but their marine representatives have mostly stayed in the littoral zone, on the continental shelves. The malacopterygians, Hubbs emphasizes, are characteristically pelagic. Abundant in fresh waters and over the continental shelf, they have also been able to go out into the open ocean, whereas the acanthopterygians are tied to the bottom. The soft-rayed fishes have retained the primitive connection of the air-bladder with the throat, and can thus reduce their buoyancy quickly when they wish to descend for a considerable distance. A few, *e.g., Arapaima,* still use it for what was probably its original function—that of a lung. In the acanthopterygians, the gas-bladder is a blind pouch and is employed variously as a slow-acting hydrostatic organ, as an ear-trumpet, or as a resonator for vocalization. Many of these bottom-bound fishes—the darters, for example—have lost it entirely.

The differentiation of the malacopterygians and acanthopterygians into originally pelagic and demersal types, respectively, did not remain at all rigid. Littoral forms belonging to both divisions learned to live beyond the edge of the continental shelf, farther and farther down the continental slopes and into the deep water of the bathyal zone. Some even went out onto the ocean floor, where the depth of the water ranges mostly between two and three miles. These inhabitants of the abyssal zone constitute the deep-sea benthos, the bottom fauna. Many families of fishes are represented in the abyssal portion of the benthos, some of them having no members elsewhere. For the most part, the abyssal fishes are archaic.

The benthonic fishes are a minority in the whole deep-sea fish population. A number of pelagic malacopterygians have sunk lower and lower to become bathypelagic, and a few have even gone all the way to the ocean floor to become a part of the benthonic fauna. Both the bathypelagic and abyssal faunas have received new additions from time to time, and will no doubt continue to do so.

The benthos (but not the richer bathypelagic fauna) contains elasmobranchs as well as teleostean species; and of course at one time the only bathybic fishes were elasmobranchs. A number of rays and sharks, and all of the bizarre chimæras, live on the continental slopes and on the ocean floor. Specimens of the weird luminous shark, *Etmopterus* (=*Spinax*) *niger,* have been taken at various levels between 100 meters and 3000 meters.

The deep-sea fishes thus comprise two distinct faunas; and the distinction is emphasized by an actual separation. The bathypelagic zone begins at a depth of about 200 meters where the pelagic zone—which is, so to say, an extension of the layer of water overlying the continental shelf—leaves off. Its lower limit is not so definite, but it is probably at about 2000 meters, and assuredly stops far short of the ocean floor. Between the bathypelagic and abyssal zones lies a thick intermediate mass of water in which only occasional wanderers occur. Though the oceans of the globe contain about 302,000,000 cubic miles of water, really only a little of this enormous space is inhabited. The sea truly teems with fish only at the shore and in the waters over the continental shelves, where such bottom-loving forms as the cod abound.

The deep-sea environment is the closest approach to nirvana that the earth provides. Below the 200-meter line, which roughly marks the edge of the continental shelf and the limit of the pelagic zone, the seasons cease to exist. Below 400 meters, there are no days—only perpetual night. No plants can grow there, and so it is dog-eat-dog—or dog-eat-carrion, for a considerable part of the food of deep-sea fishes consists of a ghastly rain of invertebrate corpses and vertebrate fragments, drifting down to them from above.

The currents in the deep waters are nowhere rapid, and toward the bottom the water is quite stagnant over much of the ocean floor—only the slow Antarctic drift has an influence so far down. The constancy of deep-sea conditions is reflected in the homogeneity of the fauna, for about the same assortment of bathypelagic species lives in one ocean as in another. Only in such enclosed holes as the Sulu Sea, and in the Mediterranean, have local, unique faunas developed.

The striking features of the bathic environment are the high water pressure, the low temperature, and the absence of light. Of these, temperature, more than anything else, rules the lives of the deep-sea fishes. Over about half of the total area of the oceans, the bottom temperature stands between 35° and 40° Fahrenheit. At depths of 1000 meters or more, it is usually at the freezing point of fresh water. Near the poles, the upper layers of water are extremely cold, but are succeeded by warmer layers beneath them, and these in turn by the paralyzing cold of the abyssal drifts. The great 'deeps', scattered here and there over the globe to the number of about fifty, are well below freezing. Some of them sound more than six miles, and their waters remain liquid because of the tremendous pressure.

Many deep-sea fishes are really, primarily, cold-water fishes. The same species, or closely related forms, may live at different depths in different places, but will be found obedient to isothermal lines drawn through that whole portion of the sea. Some genera, which are characteristic of shallow waters in polar seas, are still to be found—living far deeper in the water—in the temperate regions. Approaching the tropics, some of these arctic types live beneath two miles or more of water. A few genera, such as *Raja,* are found from pole to pole.

To a layman, the most startling feature of the bathic environment is the hydrostatic pressure. Computations are complicated by the fact that the weight of a given volume of water increases with depth—the pressures become so great that the water is actually compressed. At a depth of four miles—and a few fishes exist even there—the water is 3% heavier than at the surface. Roughly, one ton per square inch is added with each 1000 meters of depth.

Most of us have read popular accounts of submarine rescue work by skilled divers, and we know that great difficulties are involved in sending a man safely to a depth of even 100 meters in a regulation diving dress. We tend to assume that if a fish can go blithely down to many times this depth, he must have some pretty remarkable adaptations to enable him to withstand the pressure. Yet, during storms, many pelagic fishes which have no special provisions for it, sink some hundreds of feet into calmer water, later returning unharmed to their accustomed level. Though deep-sea fishes cannot be brought quickly to the surface without their 'exploding', this is because the gases in their spongy remnants of the swim-bladder, or present in solution in their body fluids, expand when released from pressure and proceed to blow the viscera out through the mouth. A fish has no great air-filled chest to be crushed, and so does not need to be kept distended by an air-compressor at the far end of a hose. He is not receiving such volumes of compressed air that his blood foams with nitrogen if he rises quickly, and no excess of oxygen in his brain makes him light-headed. For him to go downward for a few hundred feet is not at all the same as for a human diver to attempt to do so. And, for a surface fish to go *down* is not at all the same thing as for an abyssal one to come *up* (see also pp. 415-6).

Nor does the eye require any special devices for withstanding pressure, though in a captured deep-sea fish it may be bulged from the orbit by a big bubble of nitrogen which has formed behind it. The tissues of the eye, and of the whole body, are permeated by a fluid continuum in

which the hydrostatic pressure quickly follows any change in that of the water outside the animal. As far as the eye is concerned, the principal adaptations of deep-sea fishes are not to low temperature or high pressure, but to the absence of light:

The transparency of the different seas and oceans varies greatly, chiefly owing to differences in the concentration of the microscopic plankton organisms upon which all marine animal life directly or indirectly depends. A white disc two meters across, lowered parallel to the surface in mid-Atlantic, is just visible from the boat at a depth of 20 to 30 meters. In the North Sea, it is visible at such depths only on the calmest days—ordinarily, it disappears at about ten meters. The light has of course travelled twice this distance, down to the disc and back to the eye of the observer. But even making allowance for that, the water at any depth is dim from the point of view of a fish: he is not looking down at a snow-white disc as big as a table, but at a dark bottom. Or, he may be looking horizontally, at objects which receive their illumination glancingly and reflect very little of it sidewise.

The clearest of all seas is the Sargasso; and even here, the standard disc can be seen from the surface only when it is less than 66 meters down. At 370 meters in the Mediterranean, there is not enough light to affect a photographic plate. In mid-Atlantic, plates were found to be darkened at 1500 meters—but only after two hours' exposure. An eye, however sensitive to light, can take nothing but snapshots, and must have much more light than a camera whose shutter is left open while the operator goes to lunch. Even well above the 370-meter line, there is insufficient sunlight to affect a retina, let alone enough unscattered light by which to *see*—to distinguish one object from another, discriminate pattern and color, etc.

The deep-sea vertebrates and invertebrates would seem to be in about the same visual—or non-visual—predicament as the fishes of freshwater caves. It would not be surprising to find them all completely eyeless. Yet, not only do a majority of bathypelagic and benthonic fishes have eyes, but some of them, *e.g., Bathylagus, Zenion hololepis*, and *Epigonus macrophthalmus*, have (relatively) the largest eyes of any vertebrates. Few bathypelagic fishes, however monstrous they may look in a magazine illustration, are as much as a foot in length; and their eyes never compare, in absolute size, with those of large pelagic fishes or with those of large land animals. But it will be recalled (see p. 211) that the sensitivity of an eye does not depend upon its absolute dimensions, but upon the

proportioning of its dioptric parts to its receptor surface. The eyes of deep-sea fishes are probably by far the most sensitive in existence. Some of them have been claimed to have as many as 25,000,000 rods per square millimeter of retinal area.

For their ability to retain their eyes and get good use out of them, the deep-sea fishes can thank their stars. Not their astrological ones, but the stars that stud their own heads and lie in galaxies along their sides: the light-producing organs, or 'photophores' (Figs. 137, 139c; pp. 401, 404). If bioluminescence—the production of cold light by living organisms—had never been evolved in the animal kingdom, the deep sea would certainly not be fishless; but its fishes would assuredly be as eyeless as those of the caves. Excepting occasionally at the surface when there is a great congregation of luminescent plankton, there is never enough organismal luminescence to light up the ocean. The great depths, if we could visit them in a bathysphere, would hardly look to us like a moonlit landscape. We would be fortunate indeed to see as many 'stars' as are visible on a foggy night. But when one fish sees from afar the dots or blobs of light produced by another organism, the recognition of an enemy, or of prey, or of its own kind—even of its opposite sex—may be greatly facilitated.

Great numbers of marine invertebrates are luminous. Of all the species of cephalopods, about half emit light. Some shallow-water fishes have illuminant organs, which are sometimes (as in *Anomalops* and *Photoblepharon*) associated with the eyes (Fig. 134), though whether they aid the vision of their possessors is questionable. Though the light is permanent, being produced by bacteria confined in a palisade of tiny tubules, it can be concealed at will by the fish. The pelagic *Anomalops* swim in schools, flashing their lights like so many fireflies. Despite the proximity of the organ to the eye, it is probably only a social signal.

Animal luminescence, as a biological phenomenon, certainly did not originate in the deep sea; but it has reached its zenith of development among the deep-sea vertebrates and invertebrates. Beebe has computed that about two-thirds of all bathypelagic fish species—embracing about 96.5% of all individuals—are luminous. We can be sure that as any one species of fish worked its way down the continental slope, or slowly descended from the pelagic zone to the bathypelagic, it would have lost its eyes but for one thing: in the lightless realm it was invading, there were luminous organisms which had gotten there before it. The most ancient of these, at least, must have taken their luminosity down with them from the surface. In the depths, they found their light-organs val-

uable as lures, as labels, and as aids to courtship. And they kept their eyes, with which to see the other fellow's lights.

As other species followed into the depths, they too kept their eyes, for they were never entirely lacking in things to see; and in due course many of the new-comers developed photophores of their own, if they did not

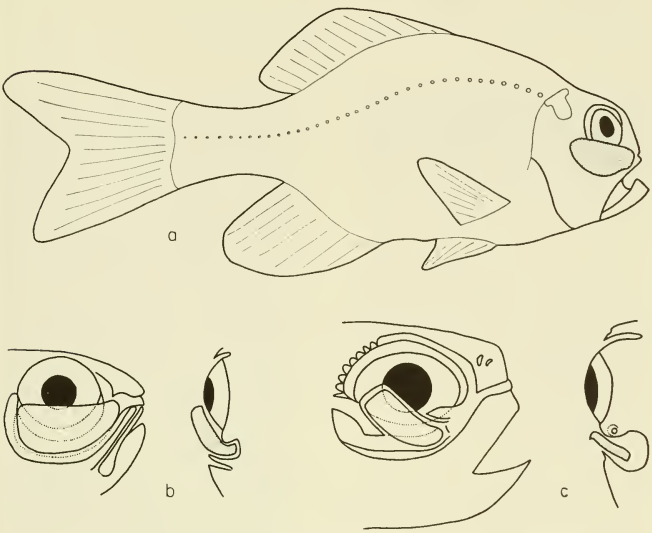

Fig. 134—Fishes with light-producing organs associated with the eyes.

a, *Photoblepharon palpebratus,* a littoral species from the Banda Sea, showing photophore (stippled). Based on photograph and drawing from Harvey. b, head of *Photoblepharon* sp., profile and section, showing photophore and the opaque 'lid' which can be drawn up over it. ×3. Redrawn from Hein. c, head of the pelagic *Anomalops katoptron,* profile and section, showing photophore and the recess into which, after being inverted, it can be withdrawn. ×3. Redrawn from Hein.

already have them. But many fishes did let their eyes go to pot. The deep-sea benthos, particularly, contains many species whose eyes are covered with opaque skin or are vestigial—*e.g., Barathronus, Typhlonus, Aphyonus,* and *Tauredophidium* among the teleosts, *Typhlonarke, Benthobatis* and *Bengalichthys* among the rays. The bottom boasts the only

vertebrate known whose eyes have gone without leaving any trace whatever: *Ipnops murrayi.* Even this fish has luminescent areas, lying on the head where the eyes ought to be; and this instance—which could be multiplied—is evidence that the photophores of a given fish are not necessarily of the slightest use in facilitating the vision of that particular fish.

Among the bathypelagic fishes, there are situations from which one can deduce something of the usual history of the eye in a species which invades the depths from the surface. Species which live farther and farther down—say, from 300 to 500 meters—tend to have larger and larger eyes and more and better photophores. Such forms are obviously trying to hang onto visual acuity, as well as to increase their sensitivity. Comes a point, however, at which the eye seems to 'quit', and becomes smaller once more. The *pupil* may continue to increase in relative size, accomplishing a further increase of sensitivity, but the shrinkage of the eye indicates that these deeply-living fishes have resigned themselves to mere light-sense vision. In some deeply bathypelagic forms such as *Cetomimus, Saccopharynx, et al,* the eye is vestigial.

These loose relationships of the eye to depth can be seen among elasmobranchs as well as among the teleosts. The chimæras of the continental slopes, and *Etmopterus,* have big eyes with huge pupils and vividly brilliant tapeta lucida. The benthonic shark *Laemargus* on the other hand has a small eye, and no tapetum; and abyssal rays may be wholly blind.

Vestigial, blind eyes are more common among the benthonic fishes; and these for the most part have also failed to develop photophores. When abyssal forms do produce light, it is usually only a faint glow due to a special luminosity of the film of slime which covers the body of any fish.

The deeply benthonic fish is better able to dispense with eyes—and to get along without photophores—than is the bathypelagic one. Life on the bottom is largely life in one plane, and the finding of food by touch and chemoreception is vastly easier. Go far enough along the bottom (if you're a fish), and you're bound to bump into something good to eat. But it does so happen that the most conspicuous of the several benthonic families of deep-sea teleosts, the archaic Coryphænoididæ or grenadiers, have retained their eyes, which are neither exceptionally small nor unusually large.

The retention of eyes by the Coryphænoididæ may be of special importance—not for these fishes themselves, but for some of their descend-

ants. Ichthyologists are coming to believe that the ubiquitous cod family originated from the grenadiers or 'rat's-tails'—developing a brand-new tail fin, and coming back up onto the continental shelf. If any *blind* abyssal fishes should return to shallow water, they could take up only habitats in which their blindness was no handicap. It is barely possible that the reef brotulids, and those which have gotten into caves (p. 388), were blind before ever they parted company with their many relations which are still on the ocean floor.

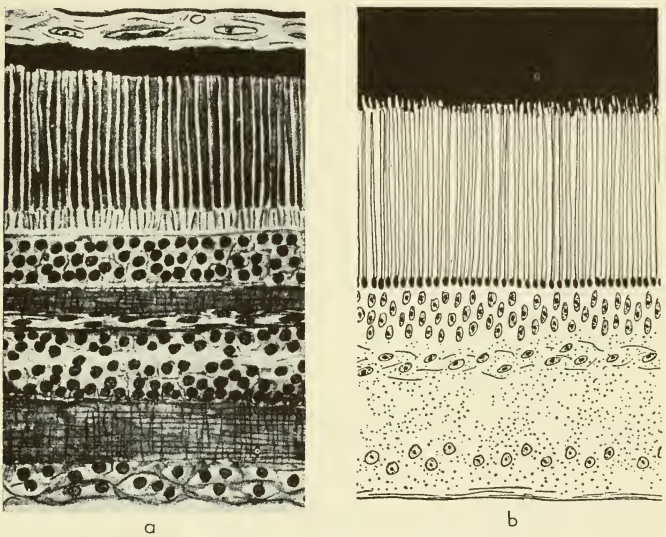

Fig. 135—Retinæ of bathypelagic teleosts.

a, a sternoptychid, *Argyropelecus hemigymnus*. ×420. After Contino. b, a myctophid, *Lampanyctus joubini*. ×500. After Verrier.

In large-eyed deep-sea fishes, everything possible has been done to increase the sensitivity of the eye to light. The pupil and lens are relatively and absolutely enlarged, cones have been largely or wholly eliminated from the retina, and the rods have been stretched to great lengths (Fig. 135) and enormously multiplied. The retinæ of *Etmopterus* and the chimæras have ten or more times as many rods per unit area as do those

of the light-bathed, small-eyed rays of the continental shelf. The retinal photomechanical changes have been eliminated in adult bathypelagic teleosts, and the pigment-epithelial cells are often devoid of pigment and processes. Summation of visual cells in optic nerve fibers is greatly increased (compare Fig. 135 with Fig. 72, p. 177).

The eyeball maintains a substantially normal external form in a majority of deep-sea species. Such normally-shaped eyes may attain a diameter equal to more than half the length of the whole head, as in *Zenion hololepis*. Beyond this point, the relative volume of the eye could scarcely be increased without serious encroachment upon other cephalic struc-

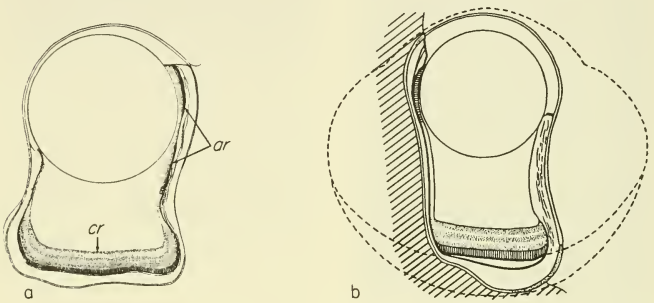

Fig. 136—Tubular eyes of deep-sea fishes.

a, *Odontostomus hyalinus*. × 13. After Brauer. *ar*- accessory retina; *cr*- chief retina. b, eye of *Argyropelecus* sp. superimposed upon outline (dotted) of normally-shaped teleost eye of the same lens-size. After Hesse.

tures. So, in many species the 'telescopic' (better, tubular) form of eyeball has been evolved:

The relationship of the tubular ocular shape to the normal can be easily expressed (see Fig. 136, also p. 212 and Fig. 84): the tubular eye is like the axial core of a normal eye, the rest of which has been thrown away to make more room in the animal's head for a very large core. But in the teleosts the tubular form is not attained, phylogenetically or developmentally, in any such simple manner. Commonly, both tubular and normal eyes occur in the same family. Both kinds even occur in different species of the same genus, as in the bathypelagic genus *Evermanella*. In at least some cases (*e.g.*, in *Argyropelecus, Ichthyococcus, Dissom-*

ma), the juvenile eye is normal or nearly so in form, and slowly becomes tubular during growth (Fig. 137).

In some forms (*e.g., Dolichopteryx, Argyropelecus, Opisthoproctus*—Figs. 137, 138a), the optic axis of the adult eye points straight upward. Here, the lens has moved dorsad and looks through transparent sclera, not true cornea, the iris and the superior ciliary body disappearing to

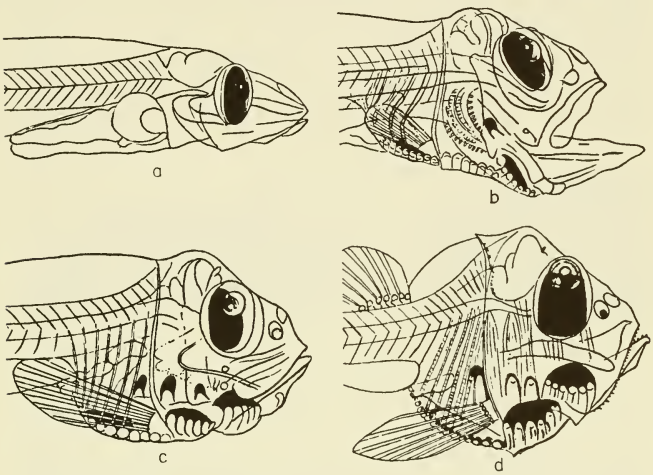

Fig. 137—Development of the tubular eye of *Argyropelecus hemigymnus*. × 14. After Contino.

a, 7.5mm. larva—'præscopic' stage (the eye aims forward). b, 10.3mm. metamorphosing larva—lens commencing its dorsad migration. c, 10.0mm. metamorphosing larva—lens continuing migration. d, 7.5mm. postlarval growth-stage—final condition (the eye, now tubular, aims upward); the ventral, pigmented organs are photophores.

allow this. The chief retina, remaining in the floor of the tube, represents the original inferior periphery of the retina. The optic nerve thus comes away from the mesial edge of the definitive retina, not from its center. A portion of the original superior retina often remains, applied to the lens as an accessory retina (Fig. 136), which is most useful for vision at a distance (see p. 257). The lens becomes so large that the iris is eliminated, the lens itself serving as a pupil. There is little or no possibility of

accommodation—the lens is often as big, in proportion to the head, as is the entire eye of such a fish, even, as *Zenion* (*v.s.*).

In such genera as *Gigantura* and *Winteria*, where the definitive tubular eye aims forward (Fig. 138b), similar intra-ocular rearrangements are the basis of the change in external form. The lens migrates nasally, of course, rather than dorsally. In *Bathytroctes* and *Platytroctes* the eyes are apparently in a half-way stage in evolution toward an eventual forward-aimed, tubular organ. *Bathytroctes* is almost unique in having a fovea in its pure-rod retina (see p. 190).

The utility of the upward aim of so many tubular eyes is not entirely clear, but it may be associated with the orientation of light-producing organs. Contrary to common supposition, the luminous organs of nearly all aquatic animals aim their light downward, not sidewise. This is true of the many luminous cephalopods mentioned above, and also of the fishes, both elasmobranchs and teleosts. Where the light comes from a broad area of skin, as in the luminous shark *Etmopterus*, this area is located on the underside. Where there are discrete photophores built like eyes, with lenses and reflectors, these aim downward—or, if located on the sides, they are so arranged that 80% of the light goes downward, not horizontally. There may be a few photophores on the back, but Hubbs has noted that these are always tiny and often appear to be degenerate in structure. In the few instances in which photophores shine frankly horizontally, they differ in numbers and arrangement in the two sexes, and here they are obviously serving primarily as sexual recognition-marks.

The downward aim of the light seems reasonable enough in a demersal species; but, it is just as characteristic of the many bathypelagic fishes which live by day at 200 meters or so and come to the surface at night—the myctophids or lantern-fishes, the sternoptychids, *Astronesthes, Cyclothone,* etc. In such vertically migratory forms, most of which school in large numbers, one might expect the light to be aimed sidewise or even upward. But whatever the significance of the orientation of photophores may be, it does seem likely that the upward aim of tubular eyes is in sympathy therewith. The deep-sea fish is not much concerned with trying to see objects illuminated by his own photophores—rather, he sees other organisms by means of *their* photogenic organs, and his own serve chiefly as a lure for prey and as an identification-tag for others of his own kind.

The parallelism of the optic axes of all deep-sea tubular eyes, (whether these are aimed upward, or forward), in itself poses a special question. Why should forms with such unsharp vision have such extreme binocu-

larity? Where there is nothing to see but a few dots of light once in a while, what price such a provision for refined space-perception? Probably, the binocularity is desirable chiefly because of the impossibility of accommodation and convergence in tubular-eyed fishes, coupled with the fact that the usual monocular cues to distance (p. 314) are lacking in the velvety blackness of the depths. And, probably, binocularity would be just as useful in the large, normally-shaped eyes of other deep-sea fishes—but in them, it could not be so easily arranged for. In the creation of the tubular form, there is opportunity to swing the visual axis through an exceptionally wide angle. Such forms as *Gigantura* have simply carried to a great extreme the same nasad asymmetry which many other animals have employed as a device for widening the binocular field (see p. 300).

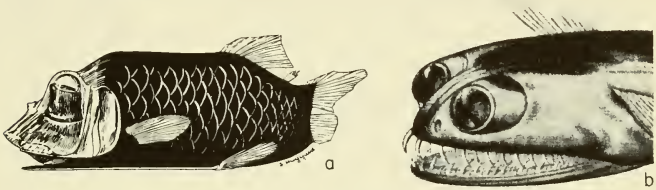

Fig. 138—Deep-sea teleosts with tubular eyes. After Brauer.

a, with eyes aimed upward (*Opisthoproctus soleatus*). Redrawn. b, with eyes aimed forward (head of 11.8cm. *Gigantura chuni*).

If the reader will imagine trying to estimate the distance of a faint dot of light in a darkroom, with one eye closed, he will appreciate the value of having bearings on such a stimulus from two angles at once. The deep-sea fish never has much more to look at than the photophores of his scanty neighbors. Monocularly, he would be about as helpless to localize them accurately, as we are to judge the distance of the stars.

Deep-Sea Larval Eyes—Ordinarily the eyes of larval deep-sea fishes are normal in structure—for larval teleost eyes—and take on any peculiar conformations, such as the tubular form, during metamorphosis and adolescence. Here, ontogeny is repetitive of phylogeny. In a few instances, however, this course of events is reversed, and a bizarre larval eye becomes an orthodox adult organ.

Most outstanding is the case of '*Stylophthalmus paradoxus*', a larva first described by Brauer in 1902. Not until 1934 was it established, by

Beebe, that the adult form of this fish is the deep-sea *Idiacanthus,* known since the work of Peters in 1876 (Fig. 139). The stylophthalmus larva has the eyeball at the end of an enormously long stalk, which is supported by a unique rod of cartilage, rooted on the skull and containing a muscular insert near its base, which enables the eye to be waved about. The rod, together with the optic nerve and the filamentous eye muscles, is ensheathed by skin which (over the front of the eyeball) contributes to the cornea in the usual way.

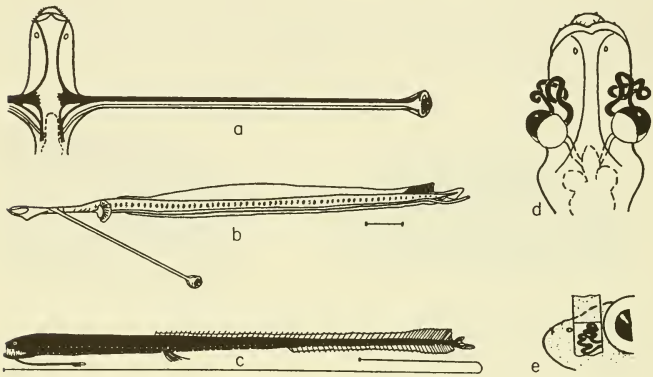

Fig. 139—*Idiacanthus fasciola.* After Beebe.

a, head of stylophthalmus larva; eye-stalk cartilage shown in black. b, c, 16mm. larva and adult female; the straight lines under the drawings express the relative body lengths. d, head of 45mm. postlarva, showing eyes retracted into head and skein-like, unshortened, eye-stalk cartilage. e, head of 35mm. transitional adolescent with skin flap raised to show coiled cartilage in anterior portion of orbit.

In post-larval stages, the eye-stalk shortens to pull the eyeball into a normal position in the head. The cartilaginous rod cannot shorten, however, so it bursts out of the stalk sheath and becomes a tangled skein (Fig. 139d), which is later tucked into the anterior part of the orbit and covered by the skin of the head (Fig. 139e). The cartilage is eventually resorbed during adolescence. The adult *Idiacanthus* eye is relatively large, but is of normal shape. The male is degenerate, never getting beyond an essentially post-larval condition except as regards the reproductive system. Unlike the female, it has a huge photophore on

the cheek, just behind the eye, which is reminiscent of the conditions in *Photoblepharon* and *Anomalops* (Fig. 134).

There are other stalk-eyed deep-sea fish larvæ, notably those of *Bathylagus, Eustomias,* and certain myctophids; but none can compare with *'Stylophthalmus'*.

In the literature of comparative ophthalmology, one deep-sea fish, *'Scopelus caninianus'* (=*Myctophum punctatum*) is erroneously credited with having 'telescopic' eyes as a larva, the eyes becoming normal in the adult. The eyes are indeed elongated in this and in some other species of *Myctophum;* but the elongation is not axial, but vertical—the vertical diameter of the eye greatly exceeding the horizontal and the axial diameters, which about equal each other. The eyeball is often pointed inferiorly, but it always rounds up during metamorphosis. In these *Myctophum* species the adult eye is aimed sidewise; but the larval eye for a time looks directly forward, and thus deserves the adjective 'præscopic' equally with *Argyropelecus* (Fig. 137a), to which this term has been applied.

The ecological significance of præscopic and stalked larval eyes is quite unknown. At first thought, one might suppose that they afforded superior perception of distance through enlargement of the binocular field or by increasing the length of the inter-ocular base of the range-finding triangle. But these larvæ are only a few millimeters in length, and their ocular frontality and relatively large inter-ocular distances are very temporary in the life-cycle, and may have no meaning for binocular vision—or at least, not the meaning they would have in sizable animals. Even among large fishes, there are some which only *seem* to have taken special pains regarding distance-perception. The hammerhead sharks, for example, have their eyes very far apart, at the ends of the 'hammers'; but they gaze only laterally, and apparently their monocular visual fields are overlapped but slightly if at all.

The Common Eel—A really amazing case is that of the common eel, *Anguilla bostoniensis.* The biological world was startled when the fairy-tale life history of this drab fish was finally worked out a few years ago. One of the most fantastic things about the eel is the cycle of change through which its eyes pass:

As we see eels during the long vegetative existence of the females in our inland ponds and streams, their eyes are small, hypermetropic, covered by a spectacle, and apparently semi-degenerate like those of

Necturus. Closer study reveals that the retina is packed with great numbers of pseudo-stratified rods, three million of them per square millimeter. This emphasis on the rods seems surprising; for though *Anguilla* is nocturnal in its feeding, its habits in fresh water would not appear to call for such an extraordinarily sensitive retina. The eel has even had to manage, somehow, to make its pupil highly contractile, something which very few other teleosts have accomplished. Moreover, the chorioid is extremely thick and the retina is full of capillaries, making it the only vascular retina which has been found outside the mammals.

The excessive retinal sensitivity and the potentially enormous nutritive supply have been explained by Franz: they are preparations for a minor miracle which takes place in a brief period of time toward the end of the eel's life. The common eel begins and ends its life as a deep-sea fish. Some months before her one and only breeding period, the eel's skin turns silvery and her eye rapidly grows until it is relatively huge. The eye is now emmetropic or possibly even myopic, and its great sensitivity to light is no more than enough to make vision possible in the next phase of the life-cycle. The formerly voluminous chorioid is finally justified by the great ocular growth which has been so rapidly accomplished by its aid.

The female eels now travel down the rivers to the sea, and they and the males make their way to the south Atlantic, in the vicinity of the West Indies. Here the eggs are laid and fertilized, whereupon both of the parent eels die. The early larvæ, which live at great depths (where, for all we know, the eggs may be laid), develop into the pelagic 'leptocephalus' stage, in which the ribbon-like, glassy-clear fishlet is quite unrecognizable as an eel. After an extremely slow and largely passive migration, the baby eel reaches the ancestral estuary as an elver—the more eel-like stage in which the eels enter fresh water. During the migration, the relatively large leptocephalus eye must be converted into an *eel* eye, thus to remain for years until its time comes to share in its owner's final preparations for reproduction and death.

Some other fishes develop through a leptocephalus stage: the tarpons, ladyfishes, and ten-pounders. Some of these may breed in brackish or fresh water; but none of them passes its adult existence as a small-eyed, nocturnal, freshwater fish. One leptocephalus (*'L. mirabilis'*) has been found which has tubular eyes. It may possibly develop into some abyssal species of eel; but the adult has not been identified. The nearest approach to the whole ocular story of the common eel is that of some lampreys. Many species of the latter pass through a silvery-bodied,

large-eyed stage, the 'macrophthalmia', in preparation for their transfer from fresh water to the sea, where their adult lives are spent. Even in some of the non-parasitic lampreys which remain always in fresh water, there are traces of a macrophthalmia stage—as a remembrance of the more complicated life history of their ancestors.

Aquatic Amphibia—Those salamanders which are permanently aquatic live in shallow water, and have little use, or special adaptation, for underwater vision. Many of these forms are secretive, living in mud or under flat stones—for example *Necturus, Cryptobranchus, Siren,* and *Amphiuma.* In such species the eye is extremely crude and disharmoniously developed, and vision is no more than a mere directional light-sense. As would be expected, the eyes of cave forms (*Proteus, Haideotriton, Typhlomolge,* adult *Typhlotriton*) are microscopic, concealed, and functionless. Some newts and axolotls, however, have quite presentable eyes. Less complex than good anuran eyes, their simplicities are not all attributable with certainty to the aquatic mode of life. But at least the spherical lens, the absence of iris folds and of the canal of Schlemm, and the emmetropic refraction in water are as probably positive adaptations as they are mere evidences of primitiveness. The few terrestrial salamanders so far studied are emmetropic in air, and hence (at least when adult) become hypermetropic in water, at breeding time.

In permanently aquatic anurans, such as the aglossal toads (*Pipa, Xenopus, Hymenochirus,* etc.) and the pseudine bufonid *Telmatobius microphthalmus,* the eyelids never develop as they do, at metamorphosis, in other frogs and toads. The eyes are very small, with round pupils. Externally they give the appearance of being almost as degenerate as those of the Central American termitivorous toads which live underground. But little seems to be on record concerning the anatomy and histology of the eyes of the above-mentioned genera.

Sirenians—Two groups of mammals have become secondarily adapted to water so completely that they are even able to breed in that medium and, unlike the seals, never need to return to the land. These are the sea-cows and the whales. Not that these animals never put their heads out of water—supposedly, it was a distant glimpse of an upreared manatee, its nursing baby cradled in its flippers, which gave some ancient sailor the raw material from which the legend of the mermaid was constructed. The old superstition is commemorated in the modern scientific name of the order Sirenia.

The existing sirenians comprise the manatees and the dugongs, the genera *Trichechus* and *Dugong* respectively. These animals are littoral, cropping grasses in shallow water, salt or brackish. In great contrast to the whales the sea-cows have an acute olfactory sense, and excellent hearing as well. Their eyes are relatively small considering the size of the animals and the turbidity of their visual medium. The eye of a six-foot *Dugong dugon* is about man-sized, with horizontal and vertical diameters of 25mm. and an axial length of 23mm. The eyes of manatees are somewhat smaller (Fig. 140).

The alterations of the eye for aquatic activity relate chiefly to the adnexa. While these structures have specialized about as far as those of whales, the globe on the other hand has lost the organization which would make it a good organ for vision through air, without taking on those characteristics which would make it really valuable under water. As compared with the whales, and particularly as compared with the seals, the sirenians have been most half-hearted in their ocular modifications for life in the water—no doubt because they were already placid herbivores (their ancestral roots are in the pro-ungulate stock) before ever they took to the sea. The condition of the modern hippopotamus, whose eyes are not his pride, affords an analogy for the probable half-way stage in the derivation of the sirenian type from a strictly terrestrial one (see p. 443).

An unusual area of the sclera shows through the lid opening—as in man, where it is also the result of a small cornea coupled with great mobility of the globe. The lids have practically lost their lashes, but they have well-developed muscles; and a retractor bulbi muscle is present so that the eye is protectible from mechanical injury. When the globe is retracted, the lids can be closed almost completely. There is disagreement as to whether a nictitating membrane is present. The tear-gland has vanished, but the Harderian gland has been retained. Its secretion is apparently not the usual sebaceous sort—Dexler and Freund describe a continuous flow of tough egg-white-like material from the eyes of a landed dugong. The cessation of this flow, as in a specimen which has drowned in a submerged net, promptly leads to a severe damaging of the cornea by the sea-water. The mucous Harderian secretion is augmented by the products of a regular pavement of special oil-glands lining the eyelids. Obviously the Sirenia are not interested in trying to recruit aqueous humor from the outside water, for they effectually prevent the latter from actually touching the cornea. Like land animals, they secrete

their aqueous, with the small number of rugose ciliary processes for which there is room on the small ciliary body (Fig. 140).

In sympathy with the 'grazing' habit the cornea is horizontally oval, being 11.0 x 7.5mm. in *Dugong;* but this is as far as the eyeball goes toward the ellipsoidality of full aquatic adaptation (compare Fig. 104, p. 259). We should expect the eyeball to be flattened—and it is, a bit, in *Trichechus;* but it is practically spherical in *Dugong.* We should also expect to find a spherical lens close to a broad, flat cornea. Instead, though the anterior segment is remarkably small, the cornea is arched and the lens is far from spherical, being the flatter in *Dugong.* In this genus, measurements of adult lenses have been given as 6.9 x 4.4mm., 7.0 x 4.0mm., etc. Different investigators have variously computed the

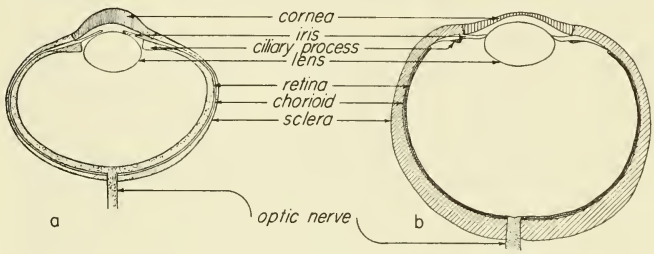

Fig. 140—Sirenian eyes.

a, a manatee, *Trichechus manatus.* x 3⅓. After Pütter. b, dugong, *Dugong dugon.* x 1⅔. Redrawn from Pettit and Rochon-Duvigneaud.

quotient of the horizontal and axial diameters of the dugong lens as 1.75, 1.57, 1.25; of the manatee lens, 1.40-1.24. These are hardly ideal relationships for under-water vision.

Though the lens is very distant from the retina and the visual field is very large—the eye of *Dugong* being strikingly human-like not only in size but in the proportioning of its parts, and with a retinal extent equalling 265° of the eyeball's circumference—the eye is not as good an air-seeing one as it looks superficially. *Dugong dugon* is five diopters myopic in air, and must be fearsomely hypermetropic in water since it has no power of accommodation. Rochon-Duvigneaud could not make out any ciliary muscle at all.

Despite the 'diurnal' gross aspect of the sirenian eye (compare Fig. 140 with Fig. 71, p. 173), it has no devices for high visual acuity. The

animals are described as being nocturnal, and their eyes are built for sensitivity (though there is no tapetum lucidum). The pupil is large, and is known to react promptly and to have a considerable excursion. It is said to be displaced ventrally; but its shape is in dispute: it has been called horizontally oval in both *Dugong* and *Trichechus,* circular in both fetal and adult dugongs, round in living manatees and horizontally oval in dead ones. Except for a few capillaries around the small, round disc, there are no retinal vessels (as in *Rhinoceros*), suggesting a low retinal metabolism and implying a pure-rod condition or the presence of but few cones at best. The visual cells have never been preserved well enough to be described accurately, but the ganglion cells are so few that summation must be great; and though the optic nerve is thick, much of its thickness is sheath.

The high sensitivity which doubtless exists is presumably required by the murkiness of the water stirred up in feeding, but it has been gained at such an expense of visual acuity that accommodation has been discarded as valueless and even static optical relationships have been allowed to come undone. All observers agree that the vision of the sirenians is wretched, and that they pay no attention to visual stimuli except to withdraw from a bright light. The low value of their eyesight to them is underlined by the fact that although they almost never look through air, they actually have *less* refractive error in that medium than in water (*v.s.*). All in all, though the rest of the sirenian body is profoundly modified for full-time marine existence, the eyeball is a disappointment. If we had only the sea-cows to go by, we should be forced to conclude that the mammalian eye is too set in its ways to depart far enough from them to give a passable imitation of the eye of a fish.

Whales—The whales have done much better. These great mammals fall into two sub-orders, the Mysticeti or baleen whales and the Odontoceti or toothed whales. The Mysticeti have specialized their feeding mechanism for straining masses of plankton organisms (largely 'krill', shrimp-like crustaceans) out of great volumes of water forced through their plates of baleen ('whalebone') by the inflatable, connective-tissue tongue. In other respects they are not more highly specialized, except as to size itself, than the Odontoceti. Although the mysticetes had toothed ancestors which were already whales, these were not odontocetes. The extinct zeuglodont whales do not appear to have been the ancestors of either of the existing groups of Cetacea, and these ancestors have yet to be found.

The two sub-orders are thus on a par taxonomically, neither being a derivative of the other. The mysticete eye is definitely less perfectly adapted to aquatic use than that of the odontocete types; but this is not because it is more primitive and has departed less far from the ancestral terrestrial condition. Rather, one must think that the toothed ancestors of the Mysticeti had better aquatic eyes than their descendants, perhaps as well adjusted as those of modern odontocetes; and that in the Mysticeti a certain degree of regression has occurred through a loss of importance of vision, correlated with the evolution of the trawling method of feeding as opposed to the active visual predation of the squid- and fish-eating Odontoceti.

The mysticetes run to large size, the pygmy among them (*Neobalæna*) being twenty feet long and the others—right whales, rorquals, the humpback, and the archaic California gray—ranging from thirty-three feet to over one hundred, the two sexes always being about equal. Their cruising speed is slow, four to six knots; and some are incapable of swimming more than about twice this fast. The great blue whale, largest of all, is said to be able to swim out of sight in a few minutes; and the finner (which feeds on herring as well as on krill) and Sei whales are capable of great speed, the latter having been clocked at thirty knots. All baleen whales have the habit of sounding, or frequently going to great depths, rhythmically diving more shallowly and spouting betweentimes. All but the very largest of them occasionally breach or leap clear of the water, an action which is purely playful and not comparable with a jack-rabbit's sky-hop. In fact, it is extremely doubtful if any whale ever puts so much as its head out of water for the purpose of peering through air. The killers (*Orcinus* etc.) among the Odontoceti are credited with thus spying out the ice floes for potential prey, and the cachalot has been claimed to stand on its flukes and revolve slowly with the head out of water, surveying the horizon. Identical actions on the part of various mysticetes, at least, are clearly due to there being insufficient room between the floes to bring the body up horizontally for spouting, necessitating an uprearing of the head, which may even be rested on the ice for a time.

Among the Odontoceti there is one type, the cachalot or sperm whale (*Physeter*), which imitates the baleen whales in many ways. It is by far the largest of its group, the male (nearly twice the size of the female) reaching sixty feet; and it is a slow swimmer—3-4 knots, 10-12 when pursued. The sperm whale moreover has the habit of sounding, and has it even more conspicuously developed than does any mysticete. *Physeter*

holds the records for both depth and duration of submergence, for it has been known to go down, at a speed of eight knots, for more than a mile, and to stay there for 105 minutes. This performance is related to the character of the prey, for the cachalot prefers to feed upon the deep-water giant squid, *Architeuthis princeps*.

The several species of beaked whales (Ziphiidæ) bridge the gap from *Physeter* and its pygmy relative *Kogia* (a latinization of 'codger') to the great family Delphinidæ, incorporating the fifty-odd species of dolphins and porpoises. These forms are relatively small, ranging from little four-foot river dolphins to animals fourteen or more feet long, the very distinct narwhal and beluga being still larger. The delphinids are pelagic, and many are notoriously playful. Porpoises are fond of racing against steamers, and are perfectly capable of keeping up with the swiftest of the fishes, the 50-knot marlins. Their rolling and frequent breaching is mere exuberance, and the eye is probably as completely useless in air as is that of a mysticete. A small, separate family of freshwater dolphins includes the susa, *Platanista,* already described as having eyes which are peculiarly degenerate (p. 210).

Optically, the whale eye has reverted to the fish type—perfectly so, in the Odontoceti. Otherwise, like that of the Sirenia, it has greeted the water not as an ancient friend, but as a new enemy. Unable to shake off all of its previous terrestrial modifications, it has superimposed upon them still other changes, to make of itself a terrestrial eye secondarily adapted to water *by being shielded from water*:

The same glandular pattern that we noted in the sea-cows has also been independently developed by the whales. Harder's gland is conspicuous, and if a lacrimal gland is present it also secretes oil. The sebaceous Meibomian glands have disappeared along with the tarsal plates in which they are embedded in other mammals, but the palpebral conjunctiva is paved with small oil-glands. This abundant provision for making the exposed part of the eyeball salt- and waterproof, and immune to friction, is aided by the cornification of the corneal epithelium, something which is seen elsewhere only in the seals, and in one or two ant-eating mammals—with a different, but obvious, meaning there. The tear-draining mechanism, sac and duct, has of course vanished. The whales are the only aquatic mammals which are quite devoid of eyelashes, and there is no nictitating membrane, no retractor bulbi.

No whale is known to be able to rotate the eyeball, though the extra-ocular muscles are present and are often quite massive. Their reten-

tion was once ascribed to their supposed value in keeping the eye warm, the idea being that all of their contractive effort goes into heat; but this theory is scouted by recent authorities. The loss of ocular rotability has had no serious consequences in itself; for the whale eye, situated always close to the angle of the jaws and thus as much as a third of the way back along the body (where the head is that large—as it often is), is quite incapable of forward vision anyway, to say nothing of binocular coöperation with its fellow.

In many cetaceans, the immobility of the eye can be blamed upon the enormously thick, stiff sheath of the optic nerve (Fig. 141). When

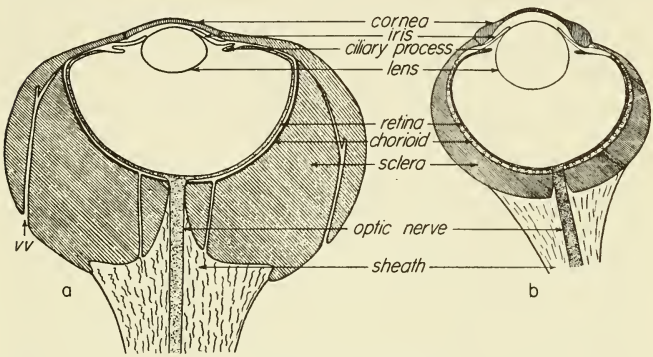

Fig. 141—Whale eyes. After Pütter.

a, a mysticete, *Balænoptera physalis*. × ½; from a 72-foot individual. *vv*, vorticose vein. b, an odontocete, *Phocæna communis*. ×1⅓.

the eye is immobile, it is only natural that if some particular direction of vision is most important, the eye should take on a permanent orientation in that direction. We have seen this to be true in owls, prosimians, and deep-sea fishes. For the whales, this most important direction appears to be downward, and the eyeball is canted ventrally or nasoventrally, with some internal asymmetry which helps out in tilting the visual axis. This is a *prima facie* reason against supposing that the whales ever care to try to see out of water.

The eyelids have altered in sympathy with the ventrad torsion of the globe. In the odontocetes they are quite equal, for the upper and lower culs-de-sac have together been shifted to equal extents around the eye in

its sagittal plane. The lids are smooth when the eye is open, indicating that their mobility has been reduced; and complete closure is probably impossible in many species. Captive porpoises have been observed never to close the lids completely for more than a few seconds at a time, even during sleep. Mysticete lids, on the other hand, are less modified. They are moderately wrinkled when open, and can perhaps be held closed without strain, though there is no more need for them to be able to close than in the case of the toothed whales. The upper lid is reduced, but the lower is puffy; for, the fornices have not shifted to let the eye aim downward as readily as in the odontocetes.

Going with its general superiority over the mysticete organ, the odontocete eye has the pupillary operculum much better developed—this being in sympathy with the predominant importance of the lower visual field, as is also the dorsal location of the tapetum lucidum in all whales. The operculum is actuated by intrinsic muscles, in contrast to the pupillary opercula of fishes—whose *modus operandi* is unknown, but which at least are known to contain no muscles. The internal shape and arrangements of the cetacean eyeball are strikingly fish-like (Fig. 141), except that it has not gone in so strongly for periscopy. The ovoid cornea is small in area, particularly in mysticetes, which by some is considered an adaptation for the conservation of heat. In the toothed whales at least, the cornea is greatly thickened at its margin, as in elasmobranchs and many teleosts. The eye is horizontally ellipsoidal, which helps to extend the horizontal visual field. The antero-posterior axis is enabled to be short, by the hardness and relative smallness of the lens, which has a refractive index approaching that in fishes. In odontocetes the lens is often a perfect ball, and never has an equatorial diameter more than 1.2 times its axial diameter. In whalebone whales the lens is at least this much flattened, and may have an equatorial diameter as much as 1.5 times the axial. In keeping with these differences, toothed whales have flatter, hence more fish-like eyes, the axis being six-tenths of the vertical diameter; while in mysticetes it is seven- or eight-tenths.

The Odontoceti have powerful ciliary muscles, sometimes even with some circular fibers as well as radial ones. Baleen whales may have no ciliary muscle at all, and never have more than from one-half to one diopter of accommodation. In compensation, they have even longer rods in their retinæ than the very long ones of odontocetes, though this difference undoubtedly exists primarily to increase sensitivity, in those whales which sound to almost lightless depths. It does not appear to be known

whether *Physeter* has extra-long rods compared with other genera of its group, most of which are shallow-swimming forms.

The most striking thing about the whale eye, as the reader's first glances at the illustrations must have shown him, is its phenomenally thick sclera. It results in the eye having actually a relatively small internal volume. Beer was unable to learn of a whale eye with an internal capacity of more than 123 cc., though whale eyes may be several inches in diameter; whereas the 37-millimeter eye of an ocean sun-fish (*Mola mola*) which he measured would hold 180 cc. The thick sclerotic coat and optic nerve sheath (Fig. 141) are generally assumed to be adaptive to the resistance of the water pressure endured by the sounding cetacean. The same thick sclera is seen in the monstrous (65-foot) whale shark (*Rhineodon typus*) and in the (also huge) basking shark (*Selache maxima*)—and the latter, at least, goes to great depths. But it is again seen in the elephants, which seldom get their heads wet.

Adaptation to Water Pressure?—The generalization has been made that animals which are very large for their kind, and whose eyes are relatively small for their size, have extremely thick scleras. In such forms as *Cryptobranchus,* possibly also in the European sturgeons, we can shrug this off as a 'disharmony'. The eyes of elephants, large sharks, and whales are too well built to make such a dismissal plausible. The thick sclera is seemingly really necessary, to maintain ocular rigidity against the pull and haul of the extra-ocular muscles. For, the absolute strength of a muscle increases as the cube of its linear dimensions; and when an object is greatly enlarged without a change of its material, its rigidity declines. A plank in the proportions of a toothpick would be far more supple than the toothpick itself.

But the whale eye, though it may be as large as a grapefruit, is supposed not to move. Does the water-pressure theory then account for its extra-thick rind? The scleras of deep-sea fishes are not thick, but we tend to suppose that these animals are somehow adjusted to the hideous pressure bearing upon them (see p. 394). In actual fact, no fish needs any sort of adjustment to meet great pressures, for there is an incompressible fluid continuum throughout his tissues, whose pressure at all times equals exactly that upon the body surface. Any surface fish which can stand cold water, and whose anatomical topography will tolerate having the swim-bladder completely collapsed without ripping anything among the viscera, can plunge slowly for a mile or for as many miles as the deeps provide. He would have to be slightly insane to do so, he might have a

struggle to rise again until the refilling of the gas-bladder had restored his buoyancy, and he might have to rise slowly to avoid the equivalent of caisson disease, due to warmed, decompressed gases foaming his blood. But he would take no harm.

The eye is in even better position (than the body as a whole) to 'stand' this pressure which does not have to be stood; for it contains no air-pockets whose compression to the point of obliteration would cause distortion. The whole body of a sperm whale must have a tremendous problem in keeping half-a-million tons from collapsing his lungs. Indeed, the diaphragm may somehow permit such a collapse, the viscera coming up into the chest cavity and squeezing so much oxygen into the blood that the animal's ability to remain so long below, and his necessity for spouting sixty times before he can sound again, are thereby accounted for. But the whale's eye certainly does not need its thick sclera just because the beast subjects himself to a great range of pressure:

Etmopterus can live as deeply as any whale ever goes; and in a specimen of this shark whose eye measured 17.0 mm. in diameter, an investigator found the sclera to be microscopically thin. In the benthonic chimæras, the sclera is actually discontinuous. In bathypelagic teleosts the scleral cartilage has been reduced from the usual extensive cup to a narrow ring. When all of these fishes which face great pressures, and great changes of pressure, have weaker eyeball-walls than their shallow-water relatives, it hardly looks as though the whales needed to thicken their scleras for pressure-resisting purposes.

The mere fact that the whale's *cornea* is relatively thin—though completely exposed to the water—is by itself enough to show that the thickness of the sclera can have no relation to high pressure as such. But the differential pressures upon various areas of the cornea, due to wave action, to ordinary swimming movements, and to quick changes in speed and direction, would deform so thin a cornea on so large an eyeball, were that cornea not supported peripherally by an immensely stiffer structure—just as a plastic watch-glass is supported by its unyielding metal bezel.

While a grape keeps its rotundity nicely while lying on a table, it would flatten out and burst if it were magnified to the size of a house—unless, that is, its skin were thickened *out of proportion*. The inordinately thick scleras of the large whales and the biggest sharks are no thicker than need be. They are a logical result of making a soft-tissued optical instrument almost too large for rigidity in the face of the buffet-

ings of the severe aquatic environment. The great whales would still need their thick scleras, even if they never left the surface at all.

Scleral cartilage has been allowed to disappear in all vertebrate groups which have allowed the eyeball to become spherical—in salamanders, snakes, and mammals. Where, as in the large whales, the globe has later ballooned and flattened, the sclera has had to be thickened very greatly; for it takes a deal of connective tissue to give the same stiffness as a much thinner piece of cartilage. It was a great piece of luck for the vertebrates to chance upon the plan, for their eyes, of a membranous sac kept turgid by internal fluid pressure. The whales have crowded that luck about as far as can safely be done.

(B) Aërial Vision

The emergence of the vertebrates upon the land necessitated several changes in the eye, which in turn made possible certain improvements which would never have been brought about in the water. Some of these changes (those of the eyeball itself) were mostly related to the major optical difference between air and water—the difference in refractive index. Other changes (those in the adnexa) were demanded by the loss of the moistening and cleansing action of water, and by the new jeopardy from sharp blows and abrasive objects.

Changes in Dioptrics — The alterations of the eyeball for vision through air were essentially optical. No longer was the eye shielded from harmful ultra-violet light, and the lens and cornea had to become able to absorb this light, or to change it by fluorescence into harmless visible light. No longer could the cornea with impunity have an irregular surface, and with the Amphibia it becomes smooth and optically perfect. Nor was a flat corneal surface any longer necessary or desirable. Exposed to air instead of to water, it became the most important refractive surface in the eyeball, where it had formerly been a nonentity. When the cornea became arched, as it first did in the amphibians, this drew the optical center of the eye forward. This in turn enlarged the image, even though the lens, now relieved of the lion's share of image-placement, became flatter and receded into the eye (*cf.* Figs. 105a and 106; pp. 261, 266). The backward shift of the lens was of inestimable importance for the future, for it placed the lens in such a relation to the ciliary body that the latter could eventually (in the Sauropsida) take over the labor of accommodation, and could accomplish this adjustment with greater speed, and over a far greater range, than had hitherto been possible.

New Extra-Ocular Structures—Associated with the typical fish eye there are only the standard oculomotor muscles and a circular lid-fold rimming the orbit. The immobile lid-fold is simply the margin of a circumocular sulcus, which is lined with a conjunctiva containing mucous goblet-cells (which persist into the mammals), but without massive glands of any kind. On taking to the land, the vertebrates were able to develop sharper vision by reason of the greater amount of light available, making possible an increase in the relative number of retinal cones. But while vision through air meant better vision, it also meant exposing the eye to desiccation which would ruin it for optical purposes and leave it an easy prey to infection. On land, too, there was a new danger of injury to the eye from dry, hard, windblown particles and from sharper collisions of all sorts than are possible in the cushioning medium of water. The vertebrates' first solution to these new problems was the production of fluid-secreting structures (the ciliary processes) inside the eyeball, and of two or more lids, new glands and new muscles outside it. In some animals this artificial aquatic environment of the cornea proved inadequate for its protection, and there was manufactured a still more perfect shielding device, the tertiary spectacle (section D).

Adnexa in Amphibia—It was pointed out in the preceding section that the great majority of Amphibia are not amphibious, but are aquatic as larvæ and terrestrial as adults. The adult amphibian, then, has need of about as complete a set of protective adnexa as does any land animal which never goes near water. If the terrestrial Amphibia fail to show such an elaborate array of ocular glands as higher forms possess, one should not be too ready to attribute this solely to primitiveness; for, after all, they mostly remain in damp situations even though on land. Salamanders are to be found in such situations as on the moist, cool soil under fallen logs. Frogs sit at the water's edge or move about in the humid air at the grass-roots of waterside meadows. Spadefoots may be very numerous in a locality, yet never seen until a prolonged rainstorm brings them out—the basis of one of the several legends of 'rains of frogs'. Other toads, and tree-frogs, may be found in the driest of places —but they are careful to keep out of the sun. Toads often burrow through dry soil into earth which is not so dry. If the skins of amphibians had permitted them to adopt drier environments, we may be quite sure that the ocular adnexa would quickly have gained the complexity shown later by the scaly sauropsidans.

Permanently aquatic salamanders and frogs, and the larvæ of all amphibians, have no lids or special ocular glands. In adult land salamanders a distinct, thick skin-fold forms an upper lid and a thinner, mobile lower lid is present. Its transparent border moves upward to close the eye, and the lid is lubricated by a row of compound glands in its lining. These may be best developed nasally and temporally; and the intervening glands may even be lacking, so that two masses of glands are isolated—the forerunners of the serous lacrimal gland (temporally) and the sebaceous Harder's gland (nasally).

In the anurans the transparent portion of the lower lid has been elaborated and is retractible within the remainder to form a Z-like fold (Fig. 106, p. 266)—often loosely termed a 'nictitating membrane' though it has no phylogenetic connection with the true nictitans of higher forms, or with that of the requin sharks. The thickened rim of the lower lid continues completely around the posterior of the eyeball as a cord, which passes through the retractor bulbi (see Fig. 143a, p. 421). When this muscle contracts, the eyeball is pulled into the head and forms a bulge in the roof of the mouth, which is of considerable aid in the swallowing of food. The resultant tug on the cord pulls out the fold of the lower lid and slips the latter up over the cornea to meet the motionless upper lid. A broad hammock-like muscle behind the eye, the levator bulbi, raises the globe once more to its normal elevated position and the lower lid automatically slips down into its folded attitude. The eye can close without complete retraction; but the retractile closure, and the muscles concerned, are important for protection against mechanical pressure and blows. The frog having no flexible neck, the eye must be able to dodge, since the head as a whole cannot! The single large gland present is considered to be the Harderian, and spreads into the orbit at metamorphosis to take a position among the muscles behind the eyeball. There are apertures, at the middle and at the nasal end of the lower lid, which communicate with a nasolacrimal or tear duct. This tube lies chiefly in the skin and runs horizontally to the small nasal cavity.

The permanently aquatic anurans (see p. 407), as might be expected, have secondarily lost the lids, and probably most or all of the special muscles and glands developed by terrestrial amphibians. The adult eye still peers through the primary spectacle of the tadpole.

The Third Lid and the Fate of the Retractor—In the Sauropsida, the lower lid still characteristically does all the work of closing the eye; but being thicker than in the frog, and moreover rendered opaque as a

rule by scales or feathers, its action results in a brief period of blindness. A third lid, the vertical 'membrana nictitans', has consequently evolved as a fold of the conjunctiva at the inner or nasal corner of the lid opening (Fig. 142). Being transparent, it can sweep the cornea from the nasal to the temporal side, to clean and moisten it, without shutting out the light. This action is of paramount importance to the scampering lizard or to the bird in flight, exposed to a stream of air which would quickly dry the cornea. There are many ornithologists who believe that the nictitans is held over the eye most or all of the time that a bird is in the air—the forerunner of the motorcyclist's goggles. The retractor bulbi muscle remains important in the reptiles and persists into the mammals. In mammals, as in the dog and cat for example, it is often divided into four slips alternating with the rectus muscles. It is lacking

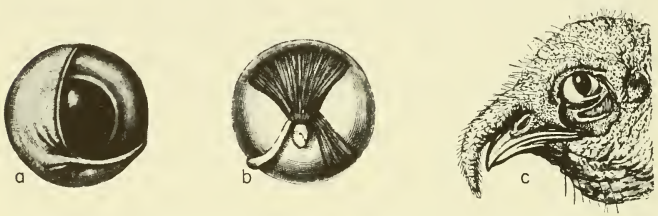

Fig. 142—The nictitating membrane or third eyelid. From Wolff, after Sutton.

a, b, front and rear views of turkey eyeball with nictitans, its tendon, and the muscles which operate it. × 1. c, the mechanism *in situ* in a dissected head.

in birds—the bird orbit hardly ever affords enough room for the retraction of the large avian eyeball, and the flexibility of the bird's neck is adequate compensation. In man, it is the heavy bony rim of the orbit, particularly the ridge bearing the eyebrow, which makes a retractor bulbi unnecessary. We may be 'hit in the eye' by a swift baseball, without the eyeball necessarily being harmed. Our erect posture may also have something to do with the loss of the retractor, which obviously is of greatest value to those large-eyed forms which, like the horse, hang their heads for a good part of the time, when feeding.

Adnexa in Sphenodon—In Sphenodon, the most generalized of living reptiles, the lacrimal gland is lacking; but a large Harderian gland moistens the cornea and lids adequately with its oily secretion. The

lower lid contains a tough tarsal plate which stiffens it and makes it slide smoothly. The nictitans contains a supporting cartilage, and its free edge continues ventrally as a cord or tendon around to the back of the eye (Fig. 143b). Here it is attached to the retractor bulbi, hence is pulled upon whenever that muscle shortens. The cord continues to an attachment on the dorsal wall of the orbit. The horizontal nasolacrimal duct has two openings or punctæ lacrimalia, on the lower-lid margin, one at the nasal end and the other several millimeters laterally from that point.

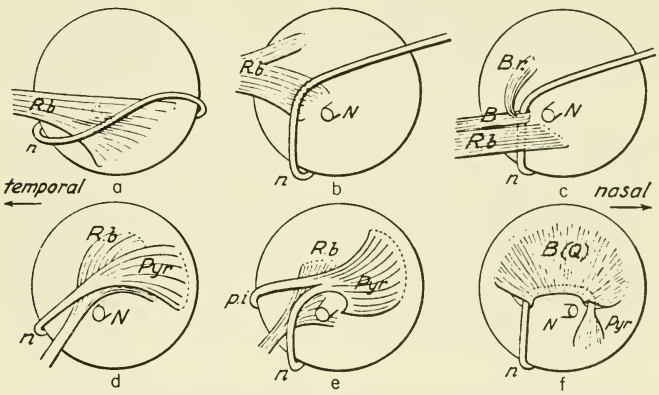

Fig. 143—Musculature of the nictitating membrane in various vertebrates. After Franz.

a, frog. b, *Sphenodon*. c, lizard (*Lacerta*). d, alligator. e, turtle. f, bird. *B, B*(*Q*)- bursalis or quadratus muscle; *B. r.*- retractor of bursalis; *n*- tendon to nictitans; *N*- optic nerve; *p. i.*- tendon to lower lid; *Pyr*- pyramidalis muscle; *R. b.*- retractor bulbi muscle.

Crocodilians—The crocodiles and their allies have gone back into the water, but they had previously developed a full panoply of terrestrial ocular accessories. They are exceptional among the reptiles in having the upper lid the larger and the more mobile, as it is in mammals. Correspondingly, the upper lid usually contains a (bony) tarsus. A cartilage-like one is present in the nictitans, but there is none in the lower lid. The large nictitans has developed a 'pyramidalis' muscle in its own tendon (Fig. 143d), which inserts on the back of the eyeball itself instead of on the orbital wall as in *Sphenodon*—a change which keeps the nictitans in a more nearly constant relation to the eyeball during eye movements.

Though it is difficult to see how the pyramidalis could have arisen as a derivative of the retractor bulbi, it is supplied by the same cranial nerve, the sixth or abducens. In fact, all of the conspicuous muscles specially developed by land animals—retractors, levators of the upper lid, depressors of the lower, operators of the nictitans—are innervated by one or another of the same three cranial nerves (third, fourth, and sixth) which supply the six primitive oculorotatory muscles (the four recti and the two obliques). Each of the newer muscles can be seen, with more or less clarity, to have been derived from some member of the original set.

The crocodilians have a lacrimal gland under the dorsal orbital roof—the lacrimal, in vertebrates generally, is most often tucked under the more mobile of the two lids—and they also have a large Harderian gland with several outlets beneath the nictitans. This situation reflects the greater importance of oily, than watery, secretions for the insulation of an essentially terrestrial eye, in an animal which has secondarily returned to water. The condition in the marine *Crocodilus porosus* is particularly interesting, as a parallel to that in the Sirenia and Cetacea; for here the conjunctiva of the lower lid is similarly paved with glands, and the nasolacrimal duct, though present, has only one puncta instead of the row of three to eight seen inside the lower lids of other crocodiles. In *Caiman sclerops* (the spectacled cayman) the upper lid shows peculiar variations, being swollen and wrinkled in some individuals and horny in others, as it is also in *C. latirostris*.

Turtles—The turtles have also 'gone back to the water', and their eyes reflect the change of habit from terrestrial to amphibious—and back to terrestrial, in the box turtles and desert tortoises. The adnexa have followed all but the last of these vicissitudes.

The lower lid is the larger, but has lost its tarsus since the wetted eye needs none. The nictitans has a small cartilage and is operated, as in crocodiles, by a pyramidalis, which sends a second tendon to the lower lid and thus acts as a levator muscle for the latter (Fig. 143e). The retractor bulbi is powerful, and may turn the eyeball almost completely over as it retracts, the nictitans and lower lid closing the eye passively at the same time. The palpebral fissure, or opening between upper and lower lids, is canted more or less so that it runs dorso-temporally to ventro-nasally of the eyeball. Though this same slant has been retained in strictly terrestrial turtles, it seems most useful to the freshwater and marine turtles, which float in a slanted position at the water surface; for when their

heads are thrust upward into the air, in line with the axis of the body, the palpebral fissure is then actually parallel to the water (see Fig. 160b, p. 547).

The lacrimal gland shows much variation. It may be compact with one or many ducts, or scattered along the length of the lower lid as in salamanders. The Harderian gland is present, with a single duct, and the nasolacrimal duct is completely absent in all turtles. A real puzzle is the enormous size of the lacrimal gland in the marine turtles which, one might think, should need none at all. It may be needed during visits to land for egg-laying; and, since males of the marine forms are rarely caught, it is not on record whether the gland is much smaller in that sex. Or perhaps the secretion is mucous or oily, and affords an analogy with the marine mammals—no one seems to know.

Lizards—In the lizards, again only the lower lid has a tarsal plate and moves, as a rule. In one anole, at least (*Anolis alligator*), the two lids do move equally. The lower lid is operated by a muscle somewhat like the orbicularis oculi of the mammals (Chapter 2, section C), but of course is not homologous therewith, since the mammalian muscle is a derivative of the facial platysma peculiar to the class. The tendon of the nictitans is enfolded by the peculiar 'musculus bursalis', from which a special retractor muscle runs to the sclera to keep the apparatus from pressing on the optic nerve (Fig. 143c). These new muscles are supplied by the sixth cranial (abducens) nerve.

The Harderian gland is large, lies nasoventrally alongside the globe, and has a single duct. The lacrimal gland lies at the temporal canthus of the palpebral fissure and has several contractile apertures. It is lacking in some lizards, notably the chameleons. These aberrant forms have no nictitans, and have the palpebral fissure greatly reduced to about the size of the pupil, the lids clinging as a broad circular fold to the surface of the huge eyeball, and turning with the eye. They seldom close except in sleep; but when they do, they meet along a straight line as usual. This situation might have arisen from one similar to that in some other lizards, for instance the family Agamidæ, where the upper and lower lids merge into one another at the canthi (as they do also in toads). In several lizards, and two turtles as well, the lower lid shows a special modification to permit vision with the eye closed, and in some burrowing and nocturnal forms the palpebral complex has been frozen into a permanent spectacle, like that of the snakes.

Snakes—The snakes show a maximum of modifications, of which the spectacle (Fig. 154, p. 456) is the most conspicuous—the others being consequences of its presence. The lacrimal gland has disappeared, and the enormous Harderian gland lies beneath and behind the eyeball. Its duct opens directly into the nasolacrimal canal, which has a single aperture (spectacled lizards have two) in the conjunctival sac, at the nasal side. As in the lizards, the distal end of the nasolacrimal duct opens within the nasal cavity, inside the accessory olfactory 'vomeronasal organ' (of Jacobson). The Harderian secretion then proceeds to the mouth cavity and contributes substantially to the saliva, which in snakes must lubricate the prey thoroughly for swallowing. Rudimentary-eyed snakes such as *Typhlops* and *Rhinophis* have even lost the connection of the nasolacrimal duct with the conjunctival sac, and the Harderian duct opens into the mouth independently of Jacobson's organ, to facilitate still further the strange function of the Harderian gland as an accessory salivary organ.

Birds—In birds, the lid opening reveals only the small cornea, so that one is easily misled as to the true size of the eyeball, and receives quite a shock upon skinning a bird for the first time! In this class of vertebrates, mobility of the upper lid reappears, in nearly half of all species. Most of these are in the higher orders, the ostrich being a conspicuous exception. The lower lid has a fibrous tarsus (except in parrots), but the nictitans has none, and is more perfectly transparent than in reptiles (except crocodiles, where its exceptional clarity would seem to go with nocturnality). In the owls and dippers, however, the nictitans is cloudy. Its inner surface is always covered by an epithelium whose surface cells are built like unicellular feathers, which improve its cleansing action. These, incidentally, are imitated in some lizards by peculiar epithelial papillæ; and the lizards have produced imitation hairs as well as feathers, for some (*e. g., Eublepharus, Coleonyx*) have 'eyelashes', manufactured from scales.

A large bursalis is present but the pyramidalis has been retained, not abandoned as by the lizards—if indeed they ever had one (Figs. 142 and 143f). The nictitans-tendon may have a very long path, because of the breadth of the globe equatorially, to reach the muscles which operate it. In the owls the eye is so long, and the orbit so snug, that the tendon courses along a groove, and over a pulley, on the surface of the eyeball (Fig. 144). As in most reptiles, the lids can be closed without the eye

retracting; but here it is because the orbit affords no room at all for a retractor bulbi.

The lacrimal gland is ventro-temporal in location, with a single duct which opens inside the lower lid. From bird to bird it shows what seem to be inconsistent variations. It is minute, as might be expected, in one group of amphibious birds (the penguins) but is particularly large in another (the dippers or water-ouzels). The owls lack it, and moreover have a very small Harderian gland, as do also their remote ancestors the goatsuckers. The very large Harderian gland of the cormorants makes good sense, for these are *marine* amphibious birds; and the avian Harderian secretion is a thick, oily emulsion which, if abundant, would shield the eye well from the osmotic and chemical effects of sea-water. In birds there are two slit-like punctæ at the nasal canthus, the upper one being the larger of the two. The penguins appear to have lost the nasolacrimal duct, for their oily tears are described as spilling down their cheeks when they are out on land.

Fig. 144 — Ventral view of right eye of an owl, *Bubo bubo*, showing nictitans tendon and its pulley. After Franz.

Mammals—In the mammals, the upper lid ordinarily comes down much more than the lower comes up. Exceptions are the elephant and hippopotamus, the camel and reindeer, the great elephant-seal, and a number of very small forms, such as the mouse. Both lids, or only the upper, may have tarsal plates. The monotreme echidnas carry out their generally sauropsidan-like ocular makeup by having a tarsus in the lower lid alone. The two lids in mammals are approximated by the annular 'orbicularis oculi' muscle, which sweeps around through both like a flattened doughnut (Fig. 17, p. 39). They are separated largely by the actions of the levator of the upper lid (a derivative of the superior rectus, which it parallels) and of the more intrinsic depressor muscle of the lower lid. In many forms, particularly primitive ones, the lids are thick and their action slow; but ordinarily they are thin and the 'blink' may be lightning-quick like the movement of a bird's nictitans. Except in forms whose binocular fields are very narrow (like the rabbit), the lids of both eyes react when only one pair is stimulated. We have all seen humans who have never learned to wink one eye!

The Meibomian glands, embedded in the palpebral tarsi, appear in the mammals for the first time. They could not well have evolved sooner, since they represent glorifications of the oil-glands associated with hairs. They are lacking in some species; and true eyelashes are absent in the elephants and whales, nearly so in the sea-cows and hippopotami.

The lacrimal gland lies near the temporal canthus. Associated as always with the more mobile of the lids, it may lie wholly above this level and has most of its 1-15 ducts opening under the upper lid. It is usually lobed or divided, as it is in man. In murid rodents it is tiny or lacking, though Harder's glands (and other glands, peculiar to rodents) are present, Harder's gland sometimes being very large and forming a cushion over the whole back half of the eyeball (mice; also, shrews). The lacrimal is said to be lacking in the pronghorn, *Antilocapra americana*. In the pig its secretion is not watery as usual, but is rich in mucus. The drainage canal is vertical and opens by two punctæ, one on or near each lid-margin at the nasal canthus, with a caruncle (Fig. 16) usually lying between them.

The nictitans has its ups and downs in the mammals. Where it is well developed, it usually has a cartilaginous tarsus, but it never has a special musculature behind the globe as in lower vertebrates. Hence, it slips over the eye only passively when the globe is slightly or markedly retracted. Contrary to logical expectations, it is most rudimented in the lower mammals and has come back to greatest usefulness in some of the higher ones. This probably explains the absence of its characteristic muscles, these having been discarded in early mammals to whom the nictitans was unimportant. It is present in the duck-bill but lacking in the echidnas, and it is vestigial in rodents and others of the lower orders such as the insectivores, primates, and 'edentates'. One of the latter group however, the aard-vark (*Orycteropus*), has a nictitans which is on a par with that of the horse—probably as a protection against the termites on which the beast feeds. The scaly ant-eaters (*Manis*) also have it decently developed.

All carnivores except the skunk, whose eye protrudes greatly like that of a mouse, have a nictitans. All can move it, though not all ever do so. In only a few could it possibly be drawn all the way over the cornea, the 'haw' of the domestic cat being a familiar example of this rare degree of development. In bears, the nictitans is not ordinarily moved, but it drifts partway over the cornea when the animal becomes sleepy. The same reaction is seen in the rhinoceroses. The white bear, however, has an excellent nictitans, and uses it as a defense against snow-blindness (as

does also the reindeer). The bear-like giant panda also has a prominent nictitans.

Ungulates all have the nictitans, though with great interspecific variations, and usually with no apparent usefulness. In the horse family, however, the nictitans is as extensive and as rapid in action as in many sauropsidans. Its retention here is attributed to the need for special protection of the eye when feeding in deep grass, and an analogous usefulness would explain its persistence in the Sirenia. It has however not been reported as being particularly well developed in the antelopes, most of which have horse-like feeding habits.

The retractor bulbi is well distributed in the lower orders of mammals, and occurs in scattered species among the higher orders. In some mammals, including all rodents, the globe is pulled back somewhat into the orbit directly by its action. In other instances, especially among the 'edentates', the eye seems rather to be pressed back passively by the lids during their periodic closures. In the hairy armadillo (*Dasypus villosus*), and also in the echidna, the lids simply swing together like a pair of gates whenever the eye is retracted, instead of sliding over the globe.

A most peculiar arrangement is seen in the opossum. As the eye closes, two vertical folds form in the conjunctiva, one at either canthus; and these close tightly over the cornea so that if the lids were then forced open, one might think the eye had been replaced by a white tumor. The writer has been fooled by a similar concealment of the retracted and rotated eyeball of a snapping turtle by proptosed conjunctiva and muscles. Another unusual phenomenon occurs in the rhinoceroses and, less conspicuously, in one species of bear (*Melursus labiatus*). Here the eyeball, every few seconds, is flicked temporally and retracted at the same time, all with lightning speed. The action appears to be a clumsy substitute for the kind of rhythmic blinking we humans perform, for it takes place too quickly to seem a means of sweeping the horizon for the detection of possible approaching enemies.

Inter-Relations of Globe and Adnexa—The evolution of lids and their associated muscles and glands by the air-breathing, air-seeing vertebrates represented primarily an effort to protect the eye by keeping it in a local aquatic environment. This method has been highly successful—too much so, in a sense, in secondarily aquatic forms, which have apparently found it impossible to dispense with as many of the concerned parts as we might think they could easily discard. An even better protection

of eyes exposed to air and to injurious terrestrial objects has been produced, in the form of a tertiary spectacle (section D), in some vertebrates—but unfortunately only in those which were absolutely driven to make this logical modification of the mobile palpebral system.

But the lids have not been without their purely optical influences upon the eyes of land animals. The very choice of an upper-lower combination instead of a nasal-temporal or diagonal one (the turtles excepted) was dictated by the predominantly vertical direction of the incident sunlight. Again, as long as the animal's eyes were carried close to the ground and exposed to bright upward reflections from the substrate, it was desirable to have the lower lid in control of eye closure. Only in those forms in which, by and large, the eyes are carried higher (crocodiles, some birds, nearly all mammals) does the upper lid become the more active of the two. In very small mammals (*e.g.*, the house mouse) the lower lid may move more than the upper, as in the creepers and crawlers of the lower classes.

The horizontal orientation of the palpebral fissure has had at least two effects upon the structure of the eyeball itself. It has allowed the development of 'ellipticity', of horizontally extended corneas and pupils, in those mammals which have great need of a wide visual field. It accounts also for the well-nigh universally vertical orientation of slit pupils in terrestrial forms. In bright light the lids, partially closed as we so often see them in a basking cat, are not unimportant in aiding the pupil to control intra-ocular illumination—as witness the fact that where the slit pupil can be entirely closed, it is most often in forms which lack mobile lids (see Chapter 9, section C). Where the slit pupil is vertical, the squinting of the lid opening at right angles to the slit makes of it a better stenopaic aperture, combatting the optical imperfections of the peripheries of lens and cornea, yet still admitting enough light because of the great retinal sensitivity of slit-pupilled eyes. It seems significant that the *vertical* orientation of the slit pupil was not finally adopted until the vertebrates came on land and developed lids (Table VI, pp. 220-1).

Peculiar Status of the Elasmobranchs—Our whole philosophy of the basis of the contrast between the fish eye (with its lack of a ciliary corona, lids, and glands, and its spherical lens in contact with a flat cornea in a shallow globe) and the typical 'air' eye (in which ciliary folds are present, the lens flattened and drawn back from an arched cornea kept moist by glands and the lids which spread their products) is rather rudely disturbed by the elasmobranchs. In some of these fishes all of the

above, 'terrestrial' characteristics are present along with others such as the salamander-like accommodation; and most of them occur in any given species of the group. If it were not almost unthinkable, we might conclude, from a cursory examination of a shark eye, that the elasmobranchs must once have lived on land and, like the whales, secondarily returned to the ocean! Surely, these peculiarities of the elasmobranch eye all have explanations other than those which hold for their seeming counterparts in the higher vertebrates; but we cannot be sure at present that we know quite all the answers.

The arching of the elasmobranch cornea and its distance from the lens appear to go simply with the method of accommodation peculiar to the group (see p. 260). The ciliary and iridic folds are probably mechanical devices for anchoring the thick zonule (whose rim covers the whole surface of the ciliary body), and not secretory—indeed, there is reason to suspect them of being absorptive. But the presence of distinct upper and lower lids in so many forms, the lower lid often having an extra transparent fold comparable to a frog's 'nictitans' (Fig. 131b, p. 382), is a deep mystery. The complex is best developed in the largely bottom-loving sharks (galeorhinid) which, if they were teleosts, might be expected to show the simpler protective device represented by the secondary spectacle. The great blue shark *Prionace glauca,* a pelagic species which is most active at night (when it hunts by scent) has been observed to blink the nictitans rapidly in bright light when pursuing prey or when otherwise excited, as though the irritation of the light were controlled somewhat by the membrane. But there is no evidence that this is always, or ever, its primary purpose. Indeed, Franz found that *Scylliorhinus* and *Mustelus* would not use their lids to shield their eyes from the strongest light, though they would struggle violently to get away from it; nor would *Raja,* capable of concealing the eye by retracting it, do so in order to avoid dazzlement.

An interesting problem awaits the investigator who attempts to correlate the palpebral complex of the elasmobranchs with something else in their biology. Its solution will be most welcome.

(C) Air-and-Water Vision

The Main Problem—Those vertebrates which wish to eat their cake and have it too, by attempting amphibious vision, have a considerable problem. If they happen to be fishes, they not only have their optical difficulties in seeing in air, but must somehow get along without the

elaborate adnexal pattern which terrestrial animals have found essential. If they happen to belong to the great sauropsidan-mammalian majority of air-and-water lookers they have no worries on this latter score; for though their lids and glands are not needed under water, neither are they any great handicap. But these secondarily aquatic forms which still cling to the land for feeding and breeding purposes have to compensate somehow for the optical loss of the cornea, when this important refractive structure is 'gone with the water'.

In attempting to combine two very diverse optical arrangements within one visual organ, amphibious vertebrates are in a position analogous to that of the twenty-four-hour animal with respect to the extremes of illumination. The arhythmic animal, be it remembered, must effect a mixture of compatible adaptations to both bright and dim light. If instead he merely 'strikes an average', he ends up not by being arhythmic and maximally independent of the rotation of the earth, but *crepuscular* and restricted more than ever in his hours of activity. Striking an average in the eye for both air and water is well enough as far as the adnexa are concerned. We see just such a situation in the Amphibia, whose half-way-evolved lids and glands allow them freedom in the air, provided that the air be humid. But half-way adaptation of the eyeball itself is impossible—there is no visual medium intermediate between water and air. However moist the atmosphere may be, seeing through it demands strictly aërial optics—and seeing through water demands, just as sternly, aquatic optics.

The problem boils down essentially to the production of an exceptional range of accommodation—sufficient, in an amphibious fish, to overcome the increased myopia which appears in the eye in air; or sufficient, in a higher vertebrate, to neutralize the hypermetropia which instantly supervenes when the cornea is immersed in water. These added demands upon the accommodation of a given amphibious animal could never be met by the mechanism characteristic of his immediate one-medium relatives, and are usually countered by supplementary devices which increase the deformation of the lens at a considerable cost in muscular effort. A very few vertebrates, however, have found easier ways of producing interchangeable aërial and aquatic systems of optics without becoming intra-ocularly muscle-bound. They meet the problem with a bare minimum of muscular exertion within the eyeball, or even with none whatever—just as a few vertebrates restricted to either aquatic or aërial vision have been clever enough to obtain good images over a range of distances without the use of dynamic accommodation at all (see pp. 254-7).

Amphibious Vision in Teleosts—It is only among the teleosts that we find fishes which spend enough time out of water to have any possible use for air-and-water vision. The number of such teleosts is surprisingly large. To mention the best known cases, there are the true flyingfishes (but *not* the 'flying' gurnards), the imitative hatchet-fishes (*Gasteropelecus, Thoracocharax, et al*), and the butterfly-fish or 'freshwater flyingfish', *Pantodon*. These forms come out of water for an appreciable fraction of a minute at a time—up to 40 seconds, in flyingfishes—though they are not amphibious inasmuch as they never come on land, or on

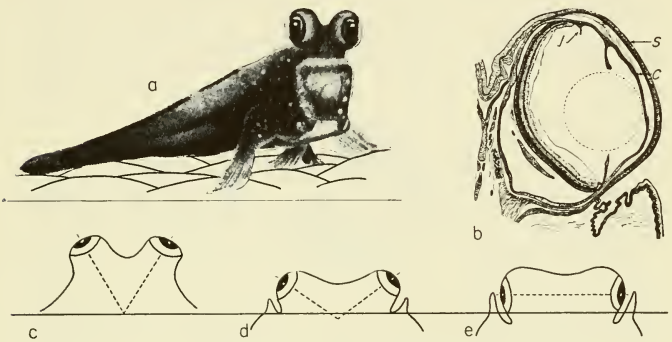

Fig. 145—*Periophthalmus koelreuteri*.

a, entire animal. × ½. After Hess. b, eye in vertical section. From Franz, after Karsten. *c*- primitive cornea; *l*- anchorage of suspensory ligament of lens; *s*- secondary spectacle. c, d, e, positions assumed by the eyes of *Periophthalmus, Boleophthalmus, et al,* showing alteration of visual lines and formation of transitory lower lids. Redrawn from Hein.

board ship, except as a fatal accident. Nothing much is known about the eyes of any of them. Then, there are such fishes as the 'climbing perch', *Anabas,* which emerge onto land for periods limited by the considerable oxygen content of their labyrinthine water reservoirs; and some blennies which perch on rocks for long periods with the tail kept in the water for respiratory purposes. Again, the eyes of these fishes are largely unstudied, though *Anabas* is known to be emmetropic in water and to have no accommodation—hence, a forbidding degree of myopia in air, with the eye probably almost useless in that medium except for brightness- and shadow-perception.

The most nearly terrestrial of fishes are certain gobies and blennies. Among the gobies, ecologically speaking, almost anything may happen. They present a wide variety of bizarre adaptations and hold a number of records of various sorts. Some of them, less than half an inch long when fully grown, are the smallest of all vertebrates. Others, *Periophthalmus, Boleophthalmus, et al,* actually prefer to spend most of their time out of water on a mud-flat exposed at low tide. Most gobies have the pelvic fins converted into an adhesive disc, and some of them cling with this to wave-dashed rocks or to the sides of burrows, like the blind *Typhlogobius* mentioned above (p. 388). It is not surprising that some surf-tossed gobies have sought still greater security by getting out of the water altogether. A still larger number of the blennies inhabit rocky places between the tide-marks. The blennies lack the suctorial attachment organ, but their amphibious members equal the amphibious gobies in pertness, fearlessness, and lizard-like agility. In keeping with these qualities they have speedier accommodation than any other fishes.

Periophthalmus and its relative *Boleophthalmus,* among the mud-skippers of the coasts of Asia, West Africa, and Polynesia, have had a good deal of attention. Their eyes are set in high turrets (Fig. 145a) and are practically on universal joints, compensating thus for the lack of a neck which becomes quite a handicap on land. They rotate under secondary spectacles which appear to be their only protection against desiccation. When deeply retracted into the head for mechanical protection, the eyes are covered by puckered skin-folds somewhat as in the rays, anglers, and turret-eyed flatfishes, which similarly have the body often in one medium (sand) while the eyes are out in another (water). When the eye of a mud-skipper is turned downward for horizontal vision like that of other fishes, the skin forms a sort of lower 'lid'. This lid is only temporary, and is abolished when the eye is elevated. The manner in which the inferior rectus and inferior oblique muscles are crossed, in the mud-skippers, makes of them a sort of cat's-cradle which raises the eye in its conning tower. There is thus no need of a special levator bulbi muscle such as the frog possesses.

In an average adult of *Periophthalmus koelreuteri,* the eyeball is 4.0 mm. in diameter with a very large (3.8 mm.) and strongly curved cornea (Fig. 145b). The lens is slightly flattened, its equatorial diameter being 1.14 times the axial. The static optics of the eye are thus those of a land animal: *Periophthalmus,* when in the air, appears to be emmetropic or even slightly hypermetropic—but the fish is then actually accommodating

maximally. When it goes under water the accommodated eye naturally becomes strongly hypermetropic. Whether perfect emmetropia can be restored in water by complete relaxation of the retractor lentis is unknown, and unlikely. The great increase in the brightness of the retinal image in air is reflected in a predominance of cones, and their distribution is clearly adaptive to the downward incidence of the sunlight. A substantial portion of the inferior half of the retina is pure-cone, the remainder duplex (with about 80% cones) except for a narrow pure-rod zone in the extreme superior periphery. The pigment epithelium is exceptionally thick, and rich in pigment. The rich cone population frees the animal from dazzlement, and makes possible a visual acuity adequate to the pursuit of its active food (largely insects) in a quite lizard-like fashion, the fish skipping about upon its stiff pectoral fins. By compari-

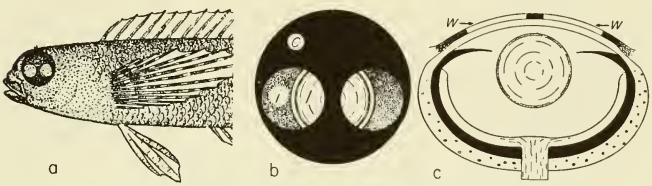

Fig. 146—*Dialommus fuscus,* an amphibious blenny. Based upon figures of Breder and Gresser. **a**, anterior end. **b**, schematic front view of eye. **c**, schematic horizontal section of eyeball. *c*- cornea; *i*- iris; *l*- lens; *w*, *w*- unpigmented 'windows' in cornea.

son with even so sharp-sighted a predator as the pike, *Periophthalmus* shows to advantage; for it has been found to have about 225,000 visual cells and 90,000 ganglion cells per square millimeter of retina, while counts in *Esox* have shown 50,600 rods, 5600 cones, and 3512 ganglion cells per square millimeter.

One of the surf-loving rock blennies, *Dialommus fuscus,* has been recently studied, though the investigators had to give up when they tried to interpret the eye. At first glance, *Dialommus* appears to have two pupils, fore and aft (Fig. 146). There is actually but one aperture in the iris itself, the two clear areas being in the *cornea* (Fig. 146c) which is otherwise heavily pigmented—a great exaggeration of the eyeshade-like dark pigmentation of the upper part of the cornea in some of the needlefishes and in *Torpedo.* Nothing is known of the refraction and accommodation of *Dialommus*, but it seems to have made an ingenious adjustment

to the greatly augmented illumination of the eye when it is in the air. Since the lens prevents the pupil from closing, the effective aperture of the eye has had to be cut down, and this has been done without sacrificing periscopy in the all-important horizontal plane. The total area of the two corneal windows is no greater than that which a single, central window would have if its diameter were equal to 1.414 ($=\sqrt{2}$) times that of one of the two little ones. But such a window would limit the visual field disastrously, particularly considering the bothersome absence of a neck. If this interpretation is correct, we must suppose that *Dialommus* does not have as insensitive (cone-rich) a retina as *Periophthalmus,* else it would not need its blacked-out cornea; but no well-preserved material, in which the retina could be studied, has become available.

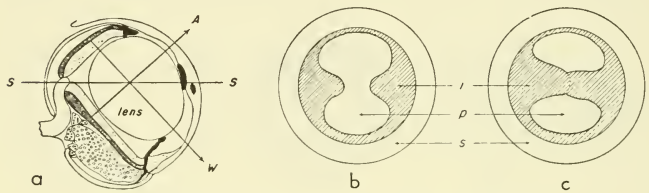

Fig. 147—*Anableps anableps,* the 'four-eyed fish'. From Walls.

a, schematic vertical section of eye. After Pütter. *S, S*- plane of water surface; *A*- line of sight upward into air; *W*- line of sight downward into water. b, pupil of 35mm. larva, with division commencing. c, pupil of adult, completely divided. After Schneider and von Orelli. *i*- iris; *p*- pupil; *s*- sclera. (See frontispiece).

Another fish—a cyprinodont this time—really does have two pupils (Fig. 147). This is the famous 'Cuatro Ojos' or four-eyed fish of northern South America and western Central America, *Anableps* (see frontispiece). The eyes are similar in the three species of this genus. The upper pupil is the larger of the two and is normally out of water; for the animal is a top-minnow, and swims sedately at the surface in quiet waters. The eye is elevated just enough in the head so that the water-line cuts it neatly in two. There are no devices to guard the upper half of the cornea against drying, so the fish periodically 'dunks' it.

Internally, the *Anableps* eye combines an aquatic optical system harmoniously with an aërial one, in a perfectly static situation (Fig. 147a). The lens is pyriform, and an imaginary extension of its long axis would pass through the superior retina and through the inferior pupil. The cur-

vatures of the lens which are used in looking through the lower pupil, into the water, are thus sharper than those aligned with the inferior retina and the superior pupil. But the inferior retina looks up through the optically effective corneal surface which is exposed to the air. Aërial and aquatic objects are thus focused simultaneously on separate regions of the retina. It is perhaps significant, in view of the impossibility of effective osmosis over a half-submerged cornea, that *Anableps* is one of the two or three teleosts known to have ciliary folds. At any rate, the eye of the Cuatro Ojos is one of the most remarkable of vertebrate eyes. The reader has probably by now given up trying to select *the* most remarkable!

Apart from the species of *Anableps,* there are other teleosts which never leave the water except in an occasional leap, but give a great deal of attention to out-of-water objects. The trout, for example, certainly sees flies before they hit the water and does not always wait for them to do so. The wise dry-fly angler arouses the trout's interest by making 'false casts', in which the fly is not allowed to touch the surface. But the trout is a piker compared with a certain very famous looker-out-of-water. This is the archer-fish, *Toxotes jaculator,* which spits a slender stream of water at an overhead insect with excellent aim, knocking it down to the surface-film of the water, from which it cannot escape. *Toxotes* is not described as ever putting its eyes out of water, and should therefore exhibit no adaptations for amphibious vision. But if the hydraulic artillery of the archer-fish is dependent upon what he can see through the surface from below, he must have a truly remarkable trigonometric range-finder in his brain to cope with the ever-varying distortion of angles, sizes, and distances (see pp. 377-9). Moreover, *Toxotes* does not, like *Anableps,* have the benefit of the glassy calm of freshwater lagoons; but the species does live in fairly calm brackish estuaries.

One of the Indian mullets, *Mugil corsula,* presents an interesting habit. This fish swims in small schools, in quiet waters. The protruding eyes are set high upon the sides of the head and are very mobile—especially antero-posteriorly. They are sometimes converged forward. The mouth is ventral, and the fish feeds upon filamentous algæ and upon caddis-flies trapped in the surface film. As the fish cruises along with the gape at the surface, the eyes are well out of water. The vision in air appears to be excellent, and the eyes, with a lens diameter-thickness ratio of 1.17 (compare *Periophthalmus,* 1.14) are definitely adapted for aërial vision. It has been suggested that this use of the eyes has been 'caused' (allowed, rather!) by the underslung mouth—present in the mud-skippers too, and

perhaps there also a predisposing factor in the raising of the eyes. On the other hand *Anableps,* being a top-minnow with a terminal mouth to begin with, has never needed to raise its eyes completely out of water in order to feed from the surface film. Like *Anableps, Mugil corsula* periodically dips its head under water to moisten the cornea.

Amphibians and Crocodilians—Probably none of the Amphibia or Crocodilini are capable of air-and-water vision. In both groups the eyes are raised in the head so that they, and the nostrils, can be in air while the rest of the body floats awash in concealment from enemies and prey. The implication is that the eyes are adjusted primarily for aërial vision and are of little or no use under water; and what little information we have bears this out. In amphibious and terrestrial amphibians the eye takes on its aërial adjustments during metamorphosis: the lids develop, the primary spectacle becomes a part of the cornea, and the latter becomes arched, while the lens departs to some extent from the perfectly spherical form which it has in the aquatic tadpole. The refractive index of the lens remains fairly high, however, with a value of 1.44-1.45 in common frogs. These animals are emmetropic in air, but have insufficient accommodation to be anything but strongly hypermetropic in water. Though the ranid frogs are the most amphibious of amphibians, they have less accommodation than the strictly terrestrial bufonid toads, which may have as much as five diopters. Some tree-frogs, just as terrestrial as the toads, may however have none at all.

Whether the crocodilians are emmetropic in either air or water is not known, but they have so little accommodation that they could not possibly have clear vision through both media. Their nocturnality and crude central images make this deficiency of no consequence to them. Spending much time basking out of water in dry, sunlit places, the crocodilians have much more perfectly 'terrestrial' adnexa than do the Amphibia.

Turtles—With the turtles, we come to the first group of amphibious vertebrates in which we can be sure that a perfect focus is attainable whether the head is immersed or above the water surface. They supplement the already superb sauropsidan machinery of accommodation (see pp. 269-79) with the powerful sphincter iridis muscle, which squeezes the front of the lens (Fig. 148) into a curvature of very short radius—a regular 'anterior lenticonus'. The range of accommodation is thus very great, easily sufficient to cancel the loss of the corneal surface. The deformation of the lens is facilitated by its extreme softness, which is maximal for all

vertebrates and exceeds that of even the lizards, whose fresh lenses will drool through one's fingers if one attempts to hold them in the hand. As might be expected, the range of accommodation is rather less in the completely terrestrial tortoises and in the thoroughly aquatic sea turtles than it is in the in-and-out pond-dwelling majority. In *Emys,* a pond genus, for example, the ciliary processes bear on the lens (Fig. 110, p. 277), and during accommodation the lens is squeezed equatorially, its diameter reduced. In the terrestrial *Testudo,* the ciliary processes touch the lens but the deformation of the latter in accommodation is much less than in *Emys,* and its diameter is not affected. In the marine *Thalassochelys,* the ciliary processes do not reach the lens, which is relatively small and is much more nearly spherical than that of other turtles. König found a transversalis muscle (p. 269) in *Emys* and *Thalassochelys,* but not in *Testudo,* whose embryonic fissure is entirely closed.

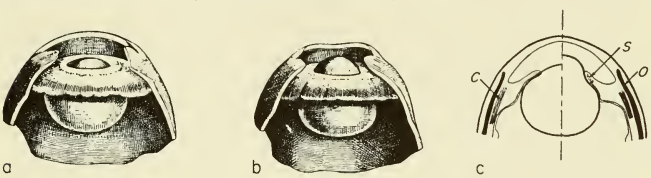

Fig. 148—Accommodation in turtles.

a, b, relaxed and accommodated conditions in *Emys orbicularis.* ×4½. From Franz, after Beer. c, diagram showing rôles of sphincter iridis and ciliary muscles in production of anterior lenticonus. *c-* ciliary muscle; *s-* sphincter iridis muscle; *o-* scleral ossicle.

The female marine turtle is in a bad way visually when she comes ashore at night to lay her eggs, for her aërial vision must be hazy and dim even if the moon is bright; and though she closes her eyes tightly when digging her nest, the reduced lids are inadequate to prevent the eyes' getting clogged with sand. All in all, she must be very glad to get back in the water, toward morning!

Since the lens of a turtle always projects through the pupil, to let the iris get a grip on it during accommodation (Fig. 148c), the pupil can actually close but little if at all. But the turtles have obtained immunity from dazzlement by eliminating nearly all of their rods, though they might perhaps have kept a well-balanced duplex retina if they had also retained efficient photomechanical changes. They are thus under some handicap in seeing under dim underwater conditions, and undoubtedly such bottom forms as the snappers and musk-turtles hunt chiefly by

touch and smell. It is perhaps because of this handicap in sensitivity that the turtles have developed the most completely transparent corneæ, humors, and lenses of any vertebrates.

Amphibious Squamates—Among the lizards there is at least one conspicuously amphibious form, the marine iguana of the Galapagos Islands, *Amblyrhynchus cristatus*. These great lizards feed mostly upon bottom sea-weeds at some distance from shore; but it was Charles Darwin who first demonstrated that their every instinct is to cling to the land or make for shore when they are attacked or frightened. It is believed that they feed in the sea out of dire necessity rather than choice. Their eyes have never been studied, but it is unlikely that they are anything but aërial in their adaptations. It will be recalled that the very thoroughly aquatic sirenians, with similar feeding habits, get along with eyes which can only be very poor-sighted under water.

There are many amphibious snakes. The most completely aquatic of them, the marine cobras (Hydrophiinæ) and the fluviatile Homalopsinæ, are practically unknown, ophthalmologically. The river snakes —*Acrochordus javanicus* for example—have the eyes toward the top of the head, but this does not necessarily mean that they are ever used out of water any more than does the same situation in the angler-fishes and star-gazers.

Years ago, Beer studied *Natrix tessellatus,* a European relative of our common water snakes, and found it to differ in two respects from terrestrial colubrids. The lens was not completely firm, and when removed from the eye it took on the shape it has in accommodation, just as does a human lens. This unusual softness permits the *tessellatus* lens (and those of our *Natrix* species, rainbow snakes, etc.?) to be squeezed by the pupillary sphincter as in the turtles, thus greatly extending the range of accommodation. In other snakes it is only those circular muscle fibers massed toward the *root* of the iris which are much concerned with accommodation, and the process (see p. 282) changes only the position of the lens and not its form. The sea-snakes contract their pupils to stenopaic pinholes when out of water, thus solving their problem somewhat as the seals (*v. i.*) have done.

Amphibious Birds—The birds had no sooner come into existence as a group than some of them, like the extinct *Hesperornis,* promptly took to the water. Many groups, and many scattered species, have become more or less aquatic since. Some are very decidedly so, and can fly as well (or

better) under water as in the air—such birds as the loons, grebes, snake-birds, auks, and penguins, all of which pursue and catch fishes. The penguins cannot fly in the air at all; and most of us have seen how much of a chore it is for a loon to 'take off'. The cormorants are also speedy fish-chasers, though they perhaps use their feet more than their wings. Still other birds swim on the surface, and up-end to feed on plants or fishes in the water beneath: ducks, coots, mergansers, etc. A host of birds, most of which can swim on the surface to rest and sometimes dive from the surface, have the habit of flying over water and plunging into it momentarily to grasp a finny prey: pelicans, gulls, terns, shearwaters, petrels, gannets, boobies, albatrosses, ospreys, sea-eagles and so on—and *one* of the cormorants, the Peruvian guano-bird.

Three kinds of birds have particularly unusual water-habits—the torrent ducks, the dippers, and the kingfishers. The kingfishers may plunge from the wing, but more commonly do so from a perch, and thus come between the flying fishers and the tall waders like the herons, whose perches are their own long legs. Their eyes, as we shall see shortly, are a little reminiscent of those of *Anableps*. The dippers are an especial phenomenon, for though no birds are so thoroughly wedded to water (they will not even fly over dry land!) they are regarded by ornithologists as having no adaptations whatever for water. The dipper or water-ouzel is simply a thrush which walks and flies unconcernedly under water to find his insect food, holding himself down when necessary by grasping stones with his feet, which even lack the ubiquitous webs of other water birds. His eyes have never been studied, but will almost certainly prove to have amphibious adaptations even though such are lacking everywhere else in the body.

In general, the eyes of all of these birds are built primarily for aërial vision. The extent to which water birds have attained underwater seeing-ability goes largely with the duration of their underwater periods, and hence, naturally, with their general bodily modification for submerged activity. Thus, the penguins head the list with eyes which are entirely devoted to water vision, with highly responsive pupils and with no special range of accommodation or other device to make them very useful in air, in which they are notoriously myopic. It has often been pointed out that a swimming penguin is quite dolphin-like in its streamlined form, with even the same color-pattern—black above and white below. Penguins are so completely adapted to water that they have hair-like feathers in enormous numbers, a whale-like blubber for heat insulation, and are

believed by non-scientific (and some scientific) observers to have their habit of eating pebbles for the purpose of ballasting, as in the case also of the elephant seal. They feed largely upon the same squids and 'krill' as do the baleen whales, but catch them individually and visually, rather than by trawling, for which they have no equipment.

Next come the cormorants, loons, auks, sea-ducks and diving ducks in general. All of these are able to secure sharply-focused images in both air and water, though not all by the same means. Last come the many species of plungers exemplified by the terns. These probably have no special ability to see in water, and characteristically make only a blind stab for the fish which they have spotted from the air. They often miss, as compared with the birds which beat the fishes at their own game of underwater swimming.

The ocular devices employed by the birds with truly amphibious vision fall into three categories, exemplified respectively by the cormorants, the diving ducks, and the kingfishers. The simplest of these devices is that of the cormorant, and is developed to about the same degree also in the booby:

The cormorant compensates for the loss of the cornea in exactly the same way as does the turtle. Its iris is the most muscular one in all the vertebrates, and the deformation of the lens by the powerful sphincter is extreme (Fig. 149). During the process, the pupil at first closes slightly, but then enlarges again as the iris tissue is rolled outward by its pressure against the lens. The lens is as soft as that of a turtle, which probably cannot be said of that of any other bird. In contrast to the few diopters of accommodation of land birds, the cormorant has 40-50 diopters—two or three times the range of the human infant, which is the most accommodating (?) of mammals, but owes its extensive range to the juvenile pliability of the lens and not to any real need.

The diving ducks, loons, and auks have much more powerful iridic sphincters than do the non-diving ducks and land birds. They have an action approaching that in the cormorants, whereas in other birds the iris molds the lens only passively as the lens is pressed against it by the ciliary processes. But these birds are as well off under water as the cormorant, and at less expense of muscular energy. Ischreyt, the leading student of their eyes, found that in all of them the nictitating membrane has a clear, lens-like central window, composed of highly refractive material which is capable of bending light rays even under water. If we compare the devices of *Anableps* and the kingfishers (*v. i.*) with bifocal

spectacles, we may compare that of the sea-duck with a 'contact lens'! Captive American mergansers have been observed to pursue their trout and salmon prey by sight. They can evidently accommodate sufficiently under water to give themselves a near point within ten feet, for they unerringly follow the movements of their victims at that distance.

The size of the cornea has been reduced by the conversion of a zone of its substance, near the limbus, into opaque sclera-like material. In the cormorant a further similarity to some aquatic mammals is seen in the thickening of the sclera at the sclerocorneal junction. In all of these birds the scleral ossicles are particularly heavy, so thick as to have marrow cavities within them like those of the hawks (Fig. 112, p. 280); and diving ducks have thick corneas. These thickenings possibly stiffen the wall of the eyeball against the shock of immersion, perhaps only support it

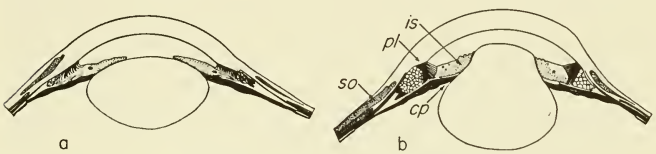

Fig. 149—Accommodation in amphibious birds.

a, anterior segment of cormorant, *Phalacrocorax* sp., in relaxation. Redrawn, modified, from von Hess. b, same as a, in accommodation, showing action of the powerful iris sphincter. Note that the fibers of the pectinate ligament are taut and that the spaces of Fontana, behind them, have become dilated by the pull of the iris.

cp- ciliary process; *is*- iris sphincter; *pl*- pectinate ligament; *so*- scleral ossicle.

against the unusual pull of the augmented accommodatory apparatus.

One part of the latter is at a low ebb in these underwater swimmers: *i. e.,* Crampton's muscle. Its function being chiefly to shorten the radius of curvature of the cornea as an aid to accommodation for near objects (p. 281), and there being no point to any manipulation of a refractive surface which is just 'not there' under water, this muscle is reduced in some amphibious species and is absent in others. There is none in the cormorants, it may be lacking or small in loons and auks, and it is small in the diving fuliguline ducks (as compared with the non-diving anatine ones). On the other hand the muscle of Brücke (Fig. 112) is massive in cormorants, stronger in diving than in non-diving ducks; and in cormorants and in the gannet (*Morus bassana*) it is most exceptional in containing circular fibers like those of the human muscle of Müller.

The kingfishers—if our interpretation of their eyes is correct—are quite alone among birds in having clear vision through both air and water without need of accommodating at all as they pass from one medium into the other. In the European *Alcedo a. atthis,* at least, Kolmer found the following situation:

The axis of the eye is somewhat shorter than its equatorial diameter. Near the ora terminalis, temporally, there is a second fovea which is as well-developed as the central one, and which sits in an outpocketing of the eyeball wall. The body of the lens is nearly symmetrical, but the lens as a whole, due to variation in the thickness of the annular pad, is strongly egg-shaped with its narrow end aimed toward the temporal fovea. The long axis of the lens is thus parallel to the palpebral fissure. The ciliary body is also strongly asymmetrical, narrowed nasally, and has particularly powerful processes around the narrow end of the oval lens. There is a well-developed sphincter iridis, but otherwise the iris and ciliary body are actually poor in muscle elements; and the chorioidal muscle-cells, said to be common in the neighborhood of the fovea centralis in other birds (see p. 281), are lacking. Kolmer's interpretation follows—how right it is, we cannot be sure at present; perhaps the investigator has been more ingenious than the bird itself:

As the kingfisher descends through the air, the prospective prey is kept in sharp focus on the central fovea of one eye, and the other eye progressively converges in sympathy. The lens is moved nasally as well as squeezed, due to the asymmetry of the ciliary body. This, together with the evaginated location of the temporal fovea, puts the latter so far from the optical center that its line of sight—not in use in air—is extremely myopic. As the bird enters the water, the cornea 'disappears' and at once the prey is sharply registered on the temporal foveæ of both eyes and thus is seen binocularly. At the same instant, the line of sight of each central fovea becomes hopelessly hypermetropic and remains so until the bird emerges into the air once more. The kingfisher seems to have improved on *Anableps,* in devising a lazy way of accomplishing an end which costs the turtle or the cormorant many a calorie.

Amphibious Mammals—The statement is often made that there is no mammal which cannot swim if tossed into water. There are a great many species which do not have to be thrown in. Brazier Howell, in his work on aquatic mammals, mentions about three score which he terms definitely (though not obliged to be) aquatic in their predilections.

These are nearly all placental mammals—there are but one aquatic monotreme (*Ornithorhynchus*) and one aquatic marsupial, the water opossum (*Chironectes*).

Of those which are amphibious—that is, excluding the whales and sea-cows—the vast majority on Howell's list are small members of the Insectivora and Rodentia. Howell believes that these, and the platypus, probably keep their eyes closed when submerged. The white bear and several mustelid carnivores are piscivorous and must use their eyes under water, but only for the European otter (*Lutra vulgaris*) have the eyes been described in any detail. The only other amphibious mammals whose eyes have had any great attention are the beaver, the hippopotamus, and particularly the Pinnipedia—seals, sea-lions, and walruses. We will consider these types in the order of their perfection of visual air-and-water adaptation:

The hippopotamus stands at the bottom of the list. From the situation in the frog and the alligator, we should at once become suspicious upon noting that the hippo's eyes are elevated like his nostrils, and may thus be kept in the air while the rest of the body is submerged. This is an aquatic adapation right enough, but it is definitely not an adaptation to aquatic vision. The adnexa have become modified, though not nearly as much as in the sea-cows. The lids form a ring bearing only traces of lashes, and close as the eye retracts. The nictitans is reduced and can cover only half of the cornea. The nasolacrimal duct has disappeared. No known aquatic or amphibious modifications occur in the eyeball itself. The hippo is unique in that it spends most of its time in the water, but does all of its feeding on land. In keeping with these habits, the pupil is horizontal like that of terrestrial ungulates, to extend the visual field somewhat in the plane in which the animal needs most of its wariness. The raising of the orbits clearly represents a device for keeping the eyes in their only appropriate medium for as much of the time as possible.

Studies on the eye of the Canadian beaver are not yet complete. The animal is essentially diurnal when quite unmolested, but does not have the yellow lens (see p. 204) characteristic of other diurnal rodents. Though the eyes are stated by Howell to be the most dorsally-directed among all rodents, the orbits form no turrets as in the hippopotamus. There is thus no *a priori* reason to suppose that the beaver cannot see in the reduced light under water. The European beaver is stated to have a cornea much thicker than the sclera, which perhaps helps the eyeball to withstand the impact on the water surface, in diving. The ciliary body

is greatly developed, and further studies may complete a picture of equal visual capacity in the two media, in each of which the beaver certainly performs as though it had excellent vision.

The otter has repeated the device of the turtles and the cormorants. The ciliary muscle is very well developed, and in addition there is an enormous sphincter in the iris which squeezes the anterior portion of the lens. The range of accommodation is unknown, but in air the eye is emmetropic or slightly hypermetropic, and the otter is known to hunt under water largely by sight despite the small size of the eye. It is entirely likely that the focusing power of the cornea is not at all missed. The adnexa of the otter appear to be quite unmodified. The nasolacrimal duct is nowadays stated to be present, though this was once denied.

The Pinnipedia, first cousins of the terrestrial carnivores, are more at home in the water than any other mammals except the whales. As with the whales, there are two large divisions of the group which differ somewhat in the character of their adaptations. The Phocidæ or 'true' seals are extremely clumsy on land owing to the profound modification of their limbs; and they have larger eyes in keeping with their habit of feeding upon relatively small prey caught in comparatively deep water. The elephant seal feeds at depths of three hundred to seven hundred feet. The Otariidæ (sea-lions or eared seals) are more comfortable on land, being still able to turn their hind feet into something like the standard mammalian walking position. They feed on fairly sizable squids and fishes, and are not believed to swim very deeply. Intermediate between these two families in many structural respects come the molluscivorous Odobænidæ, the walruses.

The visual axes of pinnipeds are canted upward to some extent rather than downward as in the strictly water-seeing cetaceans. This is probably related to their vital need of spying out the landing place before crawling out onto it—their terrestrial clumsiness is considerable of a hostage to fortune in the form of the nearest white bear. The eyes aim strongly laterally, the binocular field being about as wide as in the average terrestrial carnivore. In the elephant seal, the young animal has strongly frontal eyes which swing farther laterally during growth—the reverse of the usual ontogenetic change in the attitude of the optic axes. The lid opening is shorter than the diameter of the cornea, which compared with that of a fish is relatively small to begin with. But this is no sign of degeneracy—the seals roll and wriggle so much, in their acrobatic swimming, that they would probably be hard to approach unseen even if

they had tube vision, and lacked what little eye mobility they do have. The lids are closed by an orbicularis oculi, and there is a weakly developed tarsus in the upper lid only, with no Meibomian glands. The corneal epithelium is strongly keratinized, and in addition an abundance of protective oil is produced by the Harderian gland, which is very large, the lacrimal being only one-fourth as large (though in the fetus it is temporarily the larger of the two—ontogeny bearing out the probable course of phylogeny). Associated with the Harderian gland there is a fully-formed nictitans containing a stiffening cartilage. There is no trace of a nasolacrimal duct, even in the embryo, and the gummy tears are constantly in evidence when the animal is on land.

The eyeball is large in absolute size as well as relative to the body. In the common 'trained seal' or California sea-lion (*Eumetopias californicus*) it is 39 mm. in diameter both horizontally and vertically, the axis showing some shortening (to 35 mm.) in keeping with the fish-like optics of the eye. The axis in seals varies between 81% and 91% of the vertical globar diameter. In a half grown (ten-foot) elephant seal (*Macrorhinus*) the globe was found to be 63.2 mm. in horizontal, 65.7 mm. in vertical diameter, with a 55.7 mm. axis—thus, average with respect to the rule just stated, but constituting one of the rare examples of vertical ellipsoidality among vertebrate eyeballs. The eye of the little *Phoca vitulina* or harbor seal is a bit larger than our own, with the horizontal and vertical diameters equal, as is the rule in the group.

The cornea is circular or slightly elliptical horizontally, and is only slightly arched (except in *Macrorhinus*) over an anterior chamber which is quite un-fishlike in depth (Fig. 150), periscopy being obtained dynamically rather than statically, as mentioned above. In *Eumetopias* the cornea measures 30 by 25 mm. and its arch is 6.5 mm. high. The pinniped sclera is thickened a bit in the fundus, and the optic nerve sheath is heavy; but these structures are not all out of proportion to the internal ocular volume as they are in the much larger eyes of the whales. The chorioid is orthodox except for the great area and great number of lamellæ of the tapetum cellulosum. The ciliary body is very firmly fused to the sclera so that the chorioid cannot be pulled upon during the strong accommodation. It has circular muscle fibers as well as long, powerful meridional bundles, and bears moderately long processes which usually just reach the lens.

The lens is spherical in *Phoca*, and it never has the equatorial diameter more than 1.14 times the axial. It is proportionately much larger than in

sirenians and whales, but it is not 'nocturnal' in size. In fact, it has about the same relative diameter equatorially as that of man, being 37% of the vertical diameter of the eyeball in *Phoca vitulina* and 38.5% in *Eumetopias*. These ratios are quite distant from those obtaining in nocturnal carnivores (about 50%) and are closer to those in the twenty-four-hour ungulates (around 40%). The lens being spherical, it can be thought of as being greatly thickened; but this is an adaptation to the 'loss' of the cornea in aquatic vision, and not to nocturnality; for, the seals are diurnal. Its refractive index, like its shape, is on a par with that of fishes, and Matthiessen's ratio (p. 264) probably holds for its relationship to the retina. In consequence of the sphericity, the border of the lens epithelium reaches around past the equator of the lens onto its posterior face, as it does in fishes, aquatic amphibians and tadpoles, and toothed whales.

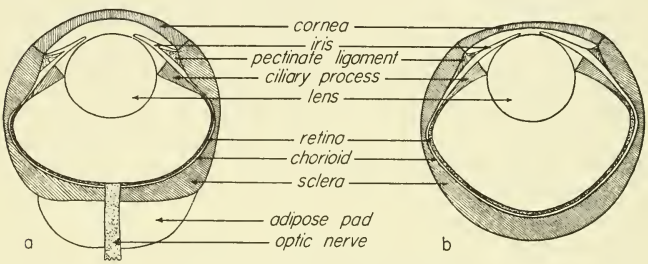

Fig. 150—Seal eyes. × 1. After Pütter.
a, an eared seal, *Otaria jubata*. b, a true seal, *Phoca vitulina*.

In view of the diurnality of the group, the apparent nocturnal adaptations of the pupil, retina, and chorioid seem paradoxical at first thought; but this paradox is the very heart of the method by which the seal accomplishes amphibious vision. The retinal rods are exceedingly long and they are commonly said to have no cones amongst them; and the retina is backed by a bright chorioidal tapetum over much of its area. These features bespeak a sensitivity which appears totally unnecessary, at least to the shallow-swimming Otariidæ. The reason for it is complex but fascinating:

In both seals and sea-lions the pupil gives some evidence of being under voluntary control, but it is ordinarily a very large circle as long as the eye is under water. The dilatator is so conspicuously developed that

some of its fibers even lead into the ciliary processes for anchorage. There is a massive sphincter, equalled among other mammals only by that of *Lutra,* and so arranged that the pupil can close to a short and narrow slit, about one millimeter by four—and does so, as a rule, the moment the head comes above water. The slit is vertical excepting in the bearded seal (*Phoca barbata*), where it is set almost horizontally—really, diagonally with the lower end toward the temple. Possibly in *barbata* it is normal to the water surface when the animal rears up, just as the oppositely-slanted palpebral fissure of turtles becomes *parallel* to the water at such times. The walrus forms an exception in that its pupil is always a broad horizontal oval like that described (by some) for the manatee, which is comprehensible in view of the similar sedentary feeding habits of the walrus.

It is reasonable enough for the pupil to close down when the eye is suddenly exposed to somewhat brighter light upon being lifted into the air—the same phenomenon is seen in the sea-snakes, for example. But why close so far, and why to a slit? Why are a nocturnal retina and a tapetum necessary for vision to continue, out of water, in the seals? They are diurnal and arhythmic in habit. There is no explanation of the matter in the literature, but at least there is a clue: Years ago, Lindsay Johnson puzzled over the astonishing degree of astigmatism which he found in both seals and sea-lions. Out of water, and under the influence of a cycloplegic drug—that is, one which dilates the pupil and paralyzes the accommodation—they showed four diopters of myopia in the vertical meridian and thirteen diopters in the horizontal, resulting in nine diopters of astigmatism against the rule (*i. e.,* with a vertical axis) as though the animals were wearing four-diopter spherical spectacles with a nine-diopter cylinder superimposed, the axis of the cylinder upright. All of this refractive error resides in the cornea, hence of course disappears in water.

In the preceding chapter we learned the virtues of a stenopaic aperture (pp. 255-6). The ideal one is the pinhole; but no vertebrate pupil which, when dilated, is a very large circle (as in the seals) can easily close to a very small pinhole. The nearest approach it can make is a slit. A slit will focus an object-point as a line which will be parallel to the slit. A cylindrical, astigmatic lens will, at its second focal plane (see Fig. 13, p. 28), image a point as a line perpendicular to the axis of the cylinder. So, if a slit pupil lies parallel to an astigmatic axis, the combination will image a point *as* a point, and will thus eliminate the astigmatism of the whole

dioptric system as effectively as a pinhole could do. At the same time, it will admit more light than will a pinhole of the same width as the slit.

The primitive seal, seeking a means of obtaining sharp images in both water and air, may have considered the usual method—that of the turtle, cormorant, and otter—but decided that it involved too much intra-ocular work to employ both ciliary muscle and iris sphincter to wring the lens. Much simpler to develop just enough accommodation to give himself emmetropia under water, and eliminate entirely the need of any great reserve of accommodation for use in seeing through the air. To make extensive accommodation in air unnecessary, he developed a high degree of corneal astigmatism, with its axis and his slit pupil so oriented as to give an approach to the performance of a pinhole camera. The quasi-pinhole reduced the retinal illumination so greatly in air that a sensitive retina, backed even by a tapetum, became necessary. Under water, the corneal astigmatism conveniently vanishes and the spherical lens, operated by a quite ordinary ciliary body, goes into action. Its accommodation has now to combat the hypermetropia which replaces the aërial emmetropia or myopia. The widened pupil lets in enough of the dimmed subaqueous light, and the seal eye is then as useful in deep water as that of a shark.

We may be sure that the system works, if not always (*Phoca barbata!*) just in this way. Considering their food and feeding habits, seals would starve without clear underwater vision. On land or ice, a seal is decidedly alert—not wholly because of his excellent olfaction. He is *visually* alert, never sleeping for more than four minutes at a time. True, the elephant seal appears near-sighted out of water, like a penguin; but even the most eye-minded vertebrates have a deadline, located afar by fear or nearby by fearlessness, to which they will allow approach without showing alarm even though they see clearly far beyond it. The elephant seal's apparent aërial myopia may really have such a basis. Under water his vision is surely good, for he feeds on swift cuttlefishes. In great contrast to *Macrorhinus,* the average seal will take flight from a man 150 yards away.

Even a wild seal is reputed to catch in its mouth a stone tossed to it. The reader may not want to believe this—and can hardly be blamed. But if he has ever watched a trained sea-lion on a dry stage going through a repertoire of catching balls, sticks, and finny rewards, he cannot doubt that the seals in general are as eye-minded, as readily able to see well through air, as he himself.

(D) The Spectacle

Injurious Substrates—As long as a vertebrate eye is held and propelled in such a way that only clean air or clean water ever ordinarily touch it, it may be adequately protected by the glandular and palpebral devices discussed in Section B. But there is only one ecological type of vertebrate that normally never encounters a substrate which is potentially, at least, injurious to the eye. This is the completely pelagic fish—the free balloon of the vertebrate kingdom. Every other kind of creature must stay on a substrate, either under air or under water, or at least come down to that substrate at more or less frequent intervals.

Where the animal's size, structure, or feeding habits place the eye in intimate relation to that substrate; and where the latter is sandy, muddy, or beset with protrusions, the lidless eyes of a fish or even the lidded ones of a land animal may be prone to injury. Where vertebrates have found themselves in such predicaments, they have usually gotten out of them by developing protective goggles.

Types of Spectacles—Wherever we find an eye which is free to rotate under a fixed, transparent covering through which it sees unimpeded, we may call that covering a goggle or spectacle. Among spectacles we can distinguish three types: primary, secondary, and tertiary. The first of these is formed by material which, though it ordinarily forms a part of the eyeball itself, has never become attached and permits the eyeball to turn freely underneath it. Secondary spectacles are anatomically practically identical with primary ones; but they represent a secondary splitting-off of the material of the spectacle from an eyeball to which it had long been joined in the ancestors. Tertiary spectacles represent distinctly extra material overlying a complete eyeball. We may recognize one or two movable coverings as tertiary spectacles, since they seem to have been historically antecedent to the latter; but we shall not include the nictitating membrane even though this is perhaps primarily spectacle-like in usefulness in one or two cases, as in the horse.

Primary Spectacles and the History of the Cornea and Conjunctiva—The primary spectacle is seen only in lampreys and strictly aquatic adult amphibians, and as a temporary affair in amphibian tadpoles (Table XI, over). It will be recalled that eyelids, where these are present, are lined with a continuation of their outer skin which is called the conjunctiva and which, far back under each lid, turns upon itself to

TABLE XI—SPECTACLES *

SIGNIFICANCE:	PRIMARY Formed by head skin overlying primitive eyeball	SECONDARY Delaminated from corneq (may simulate primary type)	TERTIARY Transparent 'window' in a movable lower lid	TERTIARY Lids fused edge-to-edge and rendered transparent
Represents future conjunctiva, corneal epithelium, part of substantia propria, as yet unfused with primitive eye	Lampreys; larval amphibians			
For streamlining—abolishes circumocular sulcus, in swift species lacking 'adipose' lids				Fishes: anchovies, *Chanos*, *Polydactylus*, et al (evolved from 'adipose' lids)
Retards dessiccation of cornea while animal is out of water		Fishes: lungfishes, eels, mudskippers, reef brotulids, purblind gobies, *Anabas*, et al		
Protects eye from sand and mud stirred up in feeding on the bottom	Lamprey and amphibian larvae; adult aquatic amphibians	Fishes: lungfishes, catfishes, *Lota*, *Cobitis*, *Halicmetus*, et al	Turtles: *Chelodina longicollis*, *Emyda granosa*	Snakes: rainbows, swamp snakes, Homalopsinae etc.
Protects eye while wriggling through desert sand; also, when sand is wind-blown			Lizards: *Chalcides*, *Trachysaurus*, *Tiliqua*, *Lygosoma fuscum*, *Mabuia vittata*, *Cabrita*, *Eremias*, et al	Lizards: *Ablepharus*, *Ophiops* Snakes: *Cerastes*, *Crotalus cerastes*, *Psammophis*, *Heterodon*, *Phyllorhynchus*, et al
Protects eye while burrowing in firm ground				Lizards: *Aniella*, Dibamidae, Amphisbænidae, Anelytropidae, Euchirotidae, some Teiidae Snakes: Leptotyphlopidae, Typhlopidae, *Xenopeltis*, fossorial boids, colubrids, elapids
Protects eye while crawling on ground in dim light		Fishes: lungfishes, eels		Lizards: geckoes, *Uroplatus*, Pygopodidae, Xantusiidae Snakes: all nocturnal, aboveground forms
An unnecessary vestige, present because produced by remote fossorial ancestor				Snakes: the great majority (diurnal, non-burrowing forms)
An expression of ocular degeneracy	Adult cave salamanders	Fishes: tiny-eyed (and some deep-sea) forms; Mormyridae, Amblyopsidae, etc.		Adult *Typhlotriton* (opaque!)

*Animals are listed under their morphological type of spectacle, and opposite the significance it has in them

form a cul-de-sac and comes forward again to fuse onto the anterior surface of the eyeball.

The epidermis of this special conjunctival skin continues over the cornea, slightly changed in the direction of a greater regularity of cell-arrangement, to form the corneal epithelium. If we seek the dermis belonging thereto, we find it not—for it has become the outer layers of the substantia propria of the cornea (Fig. 151a, b). This augmentation of the cornea, by the fusion to it of a layer of skin, was not a part of the original plan of the vertebrate eye at all. The original cornea was composed entirely of fibrous connective tissue and was simply the skin-ward portion, kept transparent throughout life, of the dural envelope enclosing the retinal cup. It quickly received two additions during early vertebrate evolution—an inner one contributed by the mesothelium of the anterior

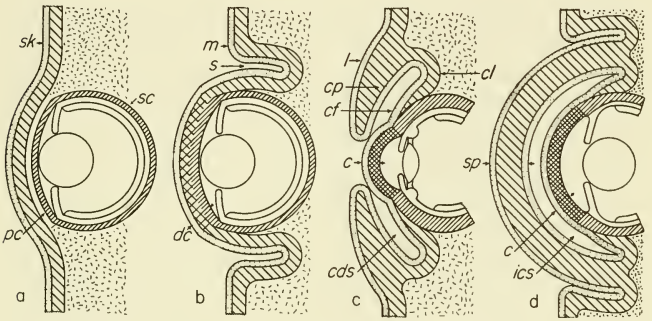

Fig. 151—Comparative morphology of the cornea, the conjunctiva, and the three categories of spectacles.

a, the primitive situation as exhibited by the lampreys. The primitive cornea *pc* is a continuation of the sclera, *sc*, and moves freely beneath a primary spectacle, which is merely a transparent window in the head skin *sk*. b, in other fishes, the skin has fused with the primitive cornea to form the definitive cornea, *dc*. Between a distinct margin *m* and the eyeball, a deep sulcus *s* creates a fold of skin which forms a 'conjunctiva fixa' where it joins the eyeball and a 'conjunctiva libera' where it lies free to permit rotation of the eyeball. A line of demarcation can still be made out between the primitive cornea and its new addition, and a secondary splitting of the cornea along this line will create a secondary spectacle, anatomically similar to the type shown at a. c, the situation in land animals; lids (*l*) have formed, so that the conjunctiva is differentiated into a conjunctiva palpebræ (*cp*), conjunctiva libera (*cl*), and conjunctiva fixa (*cf*). Beneath the lids are deep fornices or culs-de-sac (*cds*). The cornea, *c*, now shows no evidence of the dual origin of its substantia propria. d, the tertiary spectacle, *sp*, as seen in snakes and in some lizards and fishes, has been created by the edge-to-edge fusion of horizontal or vertical lids. Between the spectacle and the cornea c there is now a blind intraconjunctival space, *ics*, derived from the culs-de-sac of the lidded ancestor. This space is lined throughout by epithelium (stippled).

chamber and its basement (Descemet's) membrane, together with perhaps some connective tissue outside of the latter and homologous with the iris stroma; and an outer addition of skin whose epidermis became the corneal epithelium and whose dermis merged and fused with the outer surface of the original dural (sclerotic) tunic, which the retinal cup had carried outward with it when it grew away from the side of the brain (see p. 119).

Before this second addition was made, the eyeball had been required to remain below the level of the skin and to look out through a flat window therein. This is still the situation in lampreys (Fig. 103, p. 258), which are too primitive ever to have produced a conjunctiva—a *conjoining* of skin and eyeball. The field of vision is restricted just as is that of a man who looks through a closed window. If he opens the window and puts his head out, he can see much more.

The higher fishes could not open the window, but they could bulge it outward—make a bay-window of it, so to say. Friction on the eyeball being then intolerable, it was expedient to fuse the window onto the eye, retaining rotability by simultaneously producing, around the window, a deep circular infolding of flexible, membranous skin so that slack could be allowed to permit of turning the eyeball.

Thus the conjunctiva came into existence. The addition to the cornea was coincidental, and not produced for its own sake. The circular fold of skin overlapping the cornea all the way around proceeded to come in handy, as when the eye of a ray, for instance, is hauled back into the orbit by the retractor bulbi muscle, and the skin puckers together over the eye and protects it. Land animals found that a much neater arrangement was possible, by extending the superior and inferior margins of the fold to form permanent upper and lower lids. All of them, in their embryonic development, still form their lids from a circular, at first continuous, fold. These lids being opaque and shutting off vision whenever they are closed, some animals have added a third, almost or completely transparent lid, made by folding the conjunctiva in the nasal corner of the eye and pulling this fold—the nictitating membrane—laterally over the cornea by special means (Fig. 142, p. 420).

The triple origin of the definitive vertebrate cornea cannot ordinarily be made out in a histological preparation. The human cornea, under the slit-lamp microscope, does show a superficial extra-clear layer under the epithelium which may represent the dermal contribution to the substantia propria. The connective-tissue fiber-bundles are here somewhat

differently felted from what they are deeper in the corneal thickness; but a vertical section through the corneal thickness shows no line of demarcation in the substantia propria.

In the fishes, however, it is extremely common to find such a line, and to find that the fresh cornea can readily be peeled apart along the internal boundary surface which the line represents (Figs. 67, 105a; pp. 159, 261). It is apparently this incompleteness of fusion between the original cornea and its dermal addendum which has made it easy for many fishes and some amphibians to produce 'secondary' spectacles, which actually represent a regression to the anatomical condition in the lampreys. Even in the highest vertebrates, the corneal epithelium occasionally remembers all too well its origin as head-skin epidermis. Sheep have been known to exhibit a cornea completely covered with wool.

Secondary Spectacles—These are definitely associated in many cases with the habit of coming out of water into dry air, or of groping for food on a sandy or muddy bottom. Secondary spectacles occur in practically all amphibious fishes, and in a host of bottom species. The secondary spectacle is never horny like a tertiary one, however, and cannot offer a cornea so good a protection against desiccation. Moreover, since many bottom-feeding fishes have small, poorly developed eyes, it is impossible to say which small-eyed forms have split off a spectacle from the cornea as a positive adaptation to serve a special purpose, and which possess a spectacle as an embryonic arrest, as an evidence of a tendency of the eye to degenerate. For cave salamanders, it is particularly easy to say that the adult has a spectacle because the degenerate eye has been halted in an embryonic condition—the primary spectacle never becomes a part of the eyeball in cave forms as it does, at metamorphosis, in other salamanders. Too little is known of the mode of development of secondary spectacles in fishes—certainly many arise through an embryonic failure of fusion rather than a secondary splitting of the cornea after fusion. Such spectacles would be secondary only in the sense of a *phylogenetic* delamination of the cornea, the fishes having superimposed an inhibition upon the fusion-tendency which their ancestors permitted to operate. There is however some suggestion that many piscine conjunctivæ are fused and later separated during development, in the fact that there are usually some connective-tissue strands crossing from the surface of the residual cornea to the inside of the spectacle—such very tenuous and elastic strands (Fig. 152a, *st*) that the spectacle is able to remain motionlessly

fixed in the head skin while the cornea slides under it with the rotational movements of the eyeball.

A half-way stage in the production of a secondary spectacle seems to be exhibited by certain of the Cottidæ—*Ascelichthys rhodorus* for example. Here, the usual circumocular sulcus (Fig. 151b, *s*) has been eliminated. All that remains to represent the formerly infolded conjunctiva is a narrow zone of puckered skin surrounding the cornea and merging with the head skin at the rim of the orbit. The circular, concentric pleats in this skin afford the leeway required when the eyeball turns in the orbit. If the surface layers of the cornea continuous with the skin should split off, the pleated zone could then shrink in area and obliterate its pleats. *Ascelichthys* would then have a typical secondary spectacle.

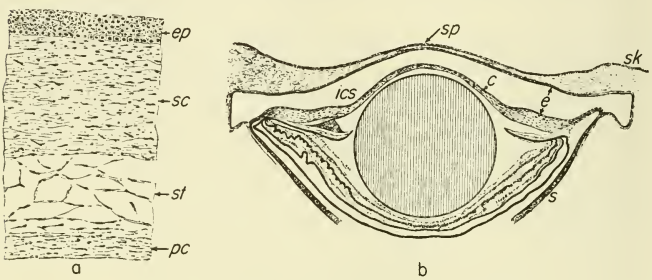

Fig. 152—Types of spectacles in teleost fishes. After Hein.

a, secondary spectacle of *Anguilla anguilla*. *ep-* epithelium of spectacle (= original corneal epithelium); *sc-* separated portion of cornea, forming mass of spectacle; *st-* strands of delicate connective tissue, which do not interfere with the movement of the eye beneath the spectacle; *pc-* primitive cornea, which remains continuous with sclera. b, tertiary spectacle and eye (collapsed) of *Engraulis* sp. *c-* cornea; *e-* epithelial lining of: *ics-* intraconjunctival space; *s-* sclera; *sk-* skin of head; *sp-* spectacle.

Tertiary Spectacles in Reptiles—The tertiary spectacle is a type with which most of us are familiar, for we have all noted the glassy stare of the reputedly lidless serpent. The snake does have lids; but they have been closed for all time, and converted into the hard, horny, dry transparent, insensitive eye scale of the herpetologists (Fig. 151d). There was long a debate as to whether this spectacle represented the upper and lower lids, the lower alone, or the nictitating membrane or third eyelid inherited from the lizards. Recent embryological work on the European grass snake and on one of the rattlesnakes has shown that after the formation

of a circular lid fold—just as in any land vertebrate—this fold gradually closes in over the eye, the aperture surrounded by it shrinking to the vanishing point and moving dorsally the while (Figs. 153, 154). Thus it is manifestly the lower lid which contributes the greater part of the spectacle. In the rattlesnake, the lid opening even becomes a normal horizontal palpebral fissure before it closes, like a healing wound, leaving no scar or trace in the finished goggle. In one snake, *Rhinophis,* a small slit is still present in the newborn young. Though it is now certain that the nictitating membrane does not even start to develop at all in the

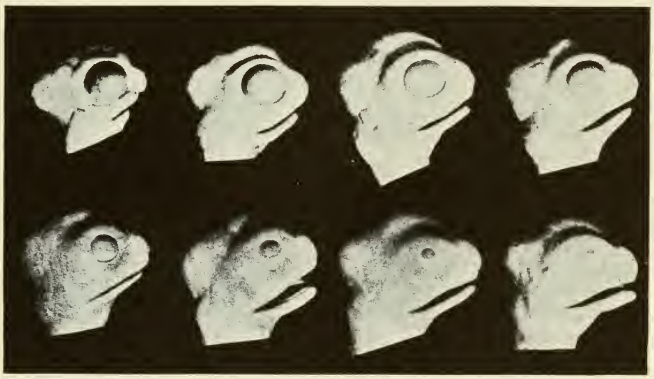

Fig. 153—Embryological formation of spectacle in a snake, *Natrix natrix.* After Schwarz-Karsten.

A circular lid-fold grows in over the cornea, its aperture at first large and concentric (upper left) but shrinking and taking up a dorsad position (lower right), eventually closing completely before birth. The finished tertiary spectacle thus comprises chiefly the lower lid, the upper lid making only a small contribution and the nictitans none at all.

snake (let alone form the spectacle), it is still a puzzle that the tear-gland associated with the upper and lower lids, the lacrimal, should be absent in snakes while the one which lubricates the third eyelid in other vertebrates—the oily Harderian gland—should be present. The Harderian secretion flows into the space between the delicate one-layered corneal epithelium and the spectacle, and drains through a duct into the nose, then into the mouth to mingle with and supplement the saliva. It is possible that the fluid has a high refractive index and some optical importance, but the optics of the tertiary spectacle remain to be worked out.

It is also possible that the snakes, being under the necessity of lubricating the apposed surfaces of the cornea and the spectacle, elected the Harderian gland simply because of the superiority of oil over water as a lubricant.

In both snakes and spectacled lizards, an outer layer of the spectacle is periodically replaced whenever the skin is shed. This renewal of the surface often comes none too soon—as one appreciates on observing the sadly scratched and dull appearance of the spectacle of a garter snake

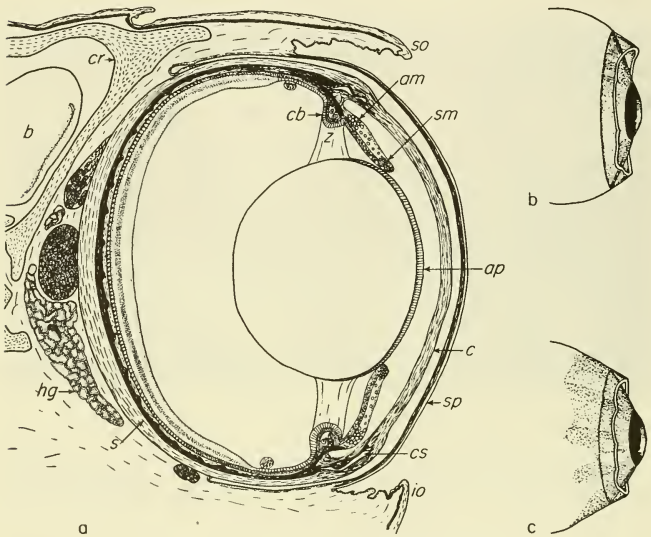

Fig. 154—The ophidian eye and its accommodation.

a, eye of European grass snake, *Natrix natrix,* in vertical section. × 22. Redrawn from Schwarz-Karsten, modified from original preparations.

am- accommodatory muscle, forming sphincter-like mass near root of iris; *ap*- anterior pad of lens; *b*- brain; *c*- cornea; *cb*- ciliary body (devoid of muscle); *cr*- cranium; *cs*- canal of Schlemm; *hg*- Harderian gland; *io*- infraocular scale; *s*- sclera (entirely fibrous—no cartilage or bone); *sm*- sphincter muscle of pupil; *so*- supraocular scale; *sp*- spectacle; *z*- zonule.

b, anterior segment of *Coluber æsculapii,* in relaxation. × 5. Redrawn from Beer.

c, same as b; in accommodation under electrical stimulation; note forward movement of lens and decrease of eyeball diameter at limbus (the dome of the cornea has been cut away, but this does not alter the course of ophidian accommodation).

inhabiting such an abrasive place as a stone wall. The formation of a milky film under the soon-to-be-shed stratum corneum of the skin, all over the body, can be particularly easily noted in the transparent spectacle, and has given rise to the widespread belief that snakes are blind when about to moult. The animal stops feeding, seeks water to soak the loosened cornified layer, and is irritable and sluggish; but how much its vision is actually dimmed is a moot point.

Outside of the snakes, the tertiary spectacle as an adaptation to locomotor substrates is found only in two turtles (where it is a temporary goggle, like a nictitans) and in a few families of lizards. Though no

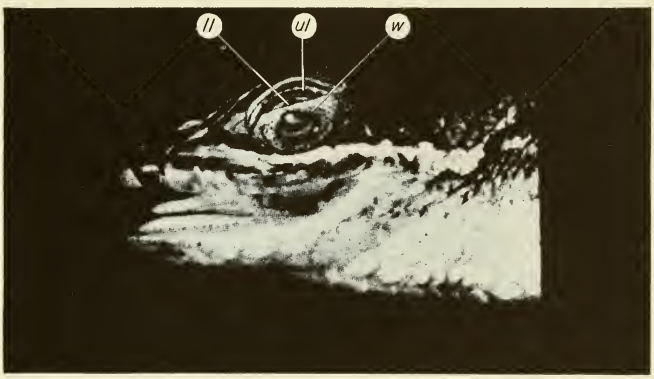

Fig. 155—The possible ancestor of the permanent tertiary spectacle: the fenestrated lower lid of a desert lizard, the scincid *Mabuia vittata*. × 6. After Schwarz-Karsten.

ll- upper edge of lower lid; *ul*- lower edge of upper lid; *w*- window in lower lid.

embryological studies have yet been made, it appears to have been formed here from the lower lid also—at least, what seems to be a halfway stage is seen in those deserticolous skinks and lacertids which have clear windows in their lower lids (Fig. 155), as do the turtles mentioned (*Emyda granosa* and *Chelodina longicollis*). When we examine the lizards for ecological correlations with the spectacle, we find that essentially two habits seem to have demanded its production: burrowing, and nocturnality. The former we can readily understand; for whether the lizard remains perpetually under firm ground or has only the problem of locomotion through shifting sand, poking the head up now and again, the

animal would be in misery without a spectacle—at least, so long as the eyes were retained in useful condition.

In some *blind* burrowing lizards (*e.g.*, Amphisbænidæ), the tertiary spectacle might seem a mere sign of ocular degeneracy—as a secondary spectacle so often is, in limicolous fishes. But if we imagine the evolution of a burrowing reptile, we see at once that the spectacle would have to antedate the blindness, and that it must have been truly protective at first. Later, of course, the spectacle came to have no meaning—when the organ it had been protecting degenerated beneath it. A morphological equivalent of the tertiary spectacle (but one which never was transparent) is seen in some moles, in which the lid opening has constricted to the vanishing point, leaving the furry skin unbroken over the vestigial eye. Similarly, in one cave salamander—*Typhlotriton spelæus*—the lids develop at metamorphosis, as usual, but then fuse edge-to-edge (except at their very centers) over the eye. Such opaque spectacles are in quite another category from those of burrowing reptiles which still had functional eyes long after they had evolved their spectacles.

The spectacles of nocturnal, non-burrowing lizards call for still another explanation. Geckoes* and night lizards (Xantusiidæ) may hide under objects, but they are not true burrowers. Most of them live far from deserts, and the desert xantusiids live under boulder flakes or in yucca tops—not in the sand. Moreover, other reptiles such as *Sphenodon,* the beaded lizards, and the crocodiles are just as nocturnal, yet have normal lids. These latter forms are large-bodied, however; and the answer to the gekkonid or xantusiid spectacle is seen in the fact that these little chaps place their eyes in constant jeopardy from gravel and stubble, amidst which they crawl under such poor visual-acuity conditions that they cannot possibly see them clearly enough to avoid them.

The spectacles of some serpents might seem to explain themselves as do those of bottom fishes, *Emyda* and *Chelodina,* or the lizards: some snakes feed in mud, some burrow, some are nocturnal. All of them reptate or crawl with the eyes very close to the potentially injurious substrate. But so do many diurnal lizards, and these have no spectacles. Most snakes are diurnal and live in above-ground habitats. Many of them are arboreal, and some are permanently aquatic. Why then do *all* snakes have spectacles when only a small minority really need them? Manifestly, because the original snake or its immediate lacertilian ancestor was nocturnal or subterranean. We shall see later (Chapter 16,

*The 'eublepharids' have mobile lids fringed with stiff lash-like scales.

section D) that the 'first snake' must indeed have lived underground, and for so long a time that the eyes degenerated very gravely. When the snakes later became a diversified, largely above-ground and diurnal group, they all had perforce to keep their spectacles whether they had any particular need for them or not.

As long as its surface is capable of being renewed, a tertiary spectacle is clearly more desirable for *any* land animal than is a pair of movable lids. We ourselves would be better off with one, and it is perhaps unfortunate that none of our direct ancestors ever had habits which made a tertiary spectacle mandatory. We are forever getting 'something in the eye'—and when this happens, we are able to deal with the situation only because we have intelligent fingers. A wild animal, in the same predicament, may claw its eye until it is injured beyond repair.

But, it would seem that nature can be persuaded to seal the terrestrial vertebrate's lids, and make them into a spectacle, only where the eyeball is imperilled far more seriously than it ever is in the vast majority of lidded vertebrates.

Tertiary Spectacles in Fishes—Spectacles assignable to this category occur in a few teleost fishes, where they differ from those of snakes and lizards in almost every particular excepting the most fundamental one of diagrammatic morphology.

In contradistinction to the secondary spectacle, so widespread among bottom forms, the tertiary type occurs only in a few pelagic fishes which are mostly close relatives of fishes in which vertical lids (p. 383) are conspicuously developed. Ichthyologists have apparently assumed that all intact coverings over piscine eyeballs represent closed, fused, vertical lids. Some taxonomic descriptions of fishes forthrightly call the spectacle, whether primary, secondary, or tertiary, an 'imperforate adipose lid'. Clearly, there is need for a more careful identification of types, as otherwise some gravely erroneous taxonomic conclusions might be drawn.

Externally, in fishes, there is no way to distinguish the three types of covering. Histologically, the primary and secondary types are discriminable only on the basis of the absence or presence of an intermediate system of delicate strands connecting the spectacle with the functional cornea (Fig. 152a). Where these strands are particularly strong, it may be possible to see them grossly upon cautiously reflecting the circumcised spectacle from the cornea. Some have claimed to find such connections between the two structures even in lampreys. However strong or weak these connective-tissue strands may be, they never prevent the cornea

from rotating somewhat under the spectacle, and the presence of eye movements associated with a motionless spectacle should never be taken as proof that the spectacle is not of the secondary type.

Histologically, the secondary and tertiary types are more easily told apart with certainty. It is obvious that if the spectacle of a given fish represents a pair of vertical lids whose aperture has been entirely abolished, there can be no connective-tissue strands crossing the space between cornea and spectacle. More important still, there is bound to be a thin epithelium lining this space, covering the cornea (where it represents the corneal epithelium—stratified, of course, in other fishes) and continuing over the inner surface of the spectacle, where it represents the epidermis of the palpebral conjunctiva (see Fig. 151d, p. 451). Such a situation has hitherto been reported for only one fish. Some years ago a Dutch investigator, Hein, described and figured an epithelium-lined subspectacular space in a clupeoid, *Engraulis* sp., and suggested that the same situation might obtain in certain other fishes, specimens of which he was unable to obtain for sectioning (Fig. 152b, p. 454).

The writer has been unable to see an epithelium on the cornea, or lining the spectacle, in sections of small museum specimens of *Engraulis mordax* kindly furnished by Dr. Hubbs; but he has found it in the 'preherring' *Chanos chanos,* and is willing to assume that the spectacles of the anchovies and their near relatives (*Anchoviella* and *Engraulis; Etrumeus*) are likewise of the tertiary type. The smallest specimens of such fishes fail to show any aperture in the spectacle, which thus either closes before hatching or is intact from its first appearance in the embryo.

In an acanthopterygian fish (*Polydactylus octonemus*), also, the writer has found the crucial epithelium. Here, it apparently consists of two layers of extremely flattened cells—in *Chanos,* there is but one layer, as in spectacled reptiles. Presumably the spectacles of any fish of the group to which *Polydactylus* belongs (the percoid family Polynemidæ) would reveal the same epithelial lining and completely empty subspectacular space. There is one clupeoid, however, whose condition cannot be so confidently predicted. This is the aberrant *Gonorhynchus,* which, though related to families which have vertical lids or tertiary spectacles, is catfish-like in habitus and habits. The spectacles of *Gonorhynchus* may prove to be of the secondary type, rather than the tertiary.

These teleostean tertiary spectacles have certainly originated from paired, independent, 'adipose' lids which have fused edge-to-edge. Their tissue is of the same sort, and they are likewise devoid of an epidermal

epithelium on the surface presented to the water. Those clupeoids which have them are next-of-kin to the herrings and their relatives, in which the vertical lids are well-nigh universal (see p. 383, Fig. 132). Functionally, tertiary spectacles are streamlining devices *par excellence*, no doubt a bit superior to the independent fore-and-aft lids from which they arose. Like the vertical lids themselves, tertiary spectacles have been separately evolved by both malacopterygian (clupeoid) and acanthopterygian fishes —always in adaptation to the habit of swift swimming, in contrast to the secondary spectacles which so much resemble them, but are characteristic of sluggish benthonic species.

Chapter 12

ADAPTATIONS TO PHOTIC QUALITY

(A) Color Vision in Animals

The Limits of the Spectrum—The first and foremost adjustment of vertebrates to the quality (that is, frequency) of light, as opposed to its quantity or intensity, was the positioning of the limits of the visible spectrum. When a student first learns that the visible spectrum occupies barely a single octave on a great keyboard of radiant-energy frequencies, he may well wonder why the eye evolved with such narrow limitations of its capacity. Since all sorts of organic substances exist which are absorbent of (*i.e.,* opaque to) frequencies far beyond the visible band in both directions, could not a much more broadly sensitive retina have been as easily devised, so that we could see much more in the world without benefit of fluoroscopic screens and infra-red-sensitive camera films?

Such a retina might have evolved, but not where the vertebrate eye took its origin—in water. Of what point to an aquatic eye, to evolve sensitivity to lights which can never strike it? By 'visible spectrum' we usually mean the assortment of contiguous wavelengths which stimulates the cones. This spectrum has complexities—of limits, peaks of maximal stimulating value, etc.—due to the behavior of the color-vision mechanism, which is far from primitive and, in land animals like ourselves, has been partly released from slavery to the properties of water. What the really primitive, pre-color-vision cone spectrum may have been like, we cannot know; but the next-most-ancient absorption spectrum is that of fish rhodopsin, which in its shortening at the red end and in the position of its maximum is clearly adjusted to the kind of light in which it has to operate. *It is thus no mere coincidence that the visible spectrum is roughly the transmission spectrum of water.* The rod spectrum is closely fitted to water, the cone spectrum a little better fitted to air.

Value and Origin of Color Vision—But the fitting of the sensitivity of the eye to the kind of light available is not the most conspicuous adjustment to photic quality. It is overshadowed by 'color vision', by which we mean the capacity to respond differently to lights which differ only in frequency. Where vertebrate color vision is a conscious process,

as it is in most cases and possibly in all, it involves differential sensations with respect to frequencies or imitative combinations of frequencies—mixtures which arouse the same sensations as single frequencies or other mixtures (see pp. 81-102).

In science, questions which begin with the word 'what' are supposed to come first, to be followed by 'how' questions—'why' queries being left largely to the philosophers. We know a great deal about the 'what' of color vision. But we know exasperatingly little about its 'how'. It is about as profitable, in the present state of knowledge, to spend thought upon its 'why':

For human beings, color vision has largely æsthetic values. If it is present in lower animals, which certainly cannot appreciate sunsets and old masters, what does it do for those animals? What was the incentive for its evolution? We cannot answer this question simply by comparing our chromatic, daylight vision with our achromatic experiences by moonlight, for too much else besides color is missing in the latter. But if we compare a black-and-white motion picture with one in color, we note at once a great difference in the visibility of things in the two. The black-and-white cameraman must be ever alert to maintain sufficient *contrast*. The heroine may report for work wearing a red blouse and a blue skirt. The cameraman may have to order one of them changed, if she is not to appear, on the screen, as if wearing a uniform! There may actually be more contrast in her costume, as far as the black-and-white film is concerned, if she wears two shades of the same color.

Color vision, then, promotes the perception of contrasts and hence, visibility. It cannot make vision capable of such complete analysis as audition (where every tone is a 'primary') can accomplish. But it does add a hundred and sixty qualities to human vision. To the first animals which developed a system of color vision, it meant the life-saving difference between being sometimes able to discriminate enemies and prey against their backgrounds, and being *usually* able to do so. 'Concealment coloration' is a counter-adaptation of some animals against the disguise-piercing searchlights of other animals' color vision; but if its evolution and perfection had ever caught up with color vision itself, zoölogists would probably not be here to worry over either phenomenon.

The Duplicity Theory (Chapter 3, section C; Chapter 7, section D) expresses the association of color discrimination with cone visual cells. We shall see shortly that there is reason to suspect that this part of the Theory does not hold at all universally; but at least no pure-rod animal

has yet been clearly demonstrated to have color vison. The tieup of cones and color vision is entirely to be expected and is not accidental. Rod vision, in the vast majority of nocturnal and twenty-four-hour animals, is even much more diffuse and unclear than in ourselves. Where visual acuity is so low as to be little more than movement- and silhouette-perception, contours and contrasts are so ill-defined to begin with that perceived color-differences could add nothing to visibility. There were almost certainly cones before there were rods, but there was probably no color vision in the vertebrate world until retinal and general ocular structure had progressed to the point where an optical basis for decent visual acuity had been laid. So, when color vision did arrive, it was only logical that it be installed in the cone mechanism. Even if the acuity of rod vision were always equal to that of cone vision (which seems to be true only of the frog), the operation of Weber's law (p. 534) would still lead to fatal reductions of contrast in the intensities of illumination suited to rod activity. Color vision could be of value only in the photopic visual mechanism of animals with *diurnal* activities.

The retinal mechanism of human color vision may be much simpler than we are fond of imagining; but on the assumption that the human retinal process is complex—so much so that it must have evolved step by step over a painfully long period of vertebrate history—biologists have long been interested in the question of where, and in what degree of completeness, color perceptions first appeared, like Christmas decorations, upon the phylogenetic tree. Psychologists have hoped, firstly, that by working out the color-vision systems of a series of vertebrate types, they might be able to identify simpler systems than the three-primary or trichromatic human one, which would then represent stages through which the human system evolved. The various dichromatic or other reduction systems of occasional humans might then be interpretable as atavisms. And, secondly—holding the quite unwarranted conviction that the chromatic photochemical system must have differentiated from *rhodopsin* —they have hoped to find, in the retinæ of lower animals, chemical waystations which would justify the assumptions of one or another of the metabolic or genetic theories of human color vision, such as the elaborate ones of Hering and Ladd-Franklin.

Before the discovery of visual-cell transmutation in 1934, the first of these hopes was quite reasonable. It may still be, and the color-vision tenet of the Duplicity Theory—that only cones can mediate color vision and that no rods do so—*may* hold quite strictly for all vertebrates, for

all we can say at present. But with transmutation (pp. 163-8) in mind, we know that we must be less ready than ever before to assume this, and we must realize that even if a series of color-vision systems is ever found in vertebrates, only a far more accurate knowledge of the course of phylogeny than we now have can ever make it possible to say which simpler systems are stages in the evolution of human color-vision, and which of them are independent inventions.

For, just as it is certain that rhodopsin has been invented many times, it is almost certain that color vision has been repeatedly evolved in different vertebrate groups. When the geckoes' rods were secondarily made from ancestral lizard cones, was color vision lost? If so, then has it returned in the tertiarily diurnal gecko *Phelsuma*? Do snakes have color vision—and if so, could it conceivably have been inherited directly from the lizards through the snakes' underground, degenerate-eyed beginnings? Did those first placental mammals keep any of the cones (and color vision) of their ancestors? Or is it because the cones (and color vision) of the placental mammals and primitive snakes were reinvented by those groups, that there are no oil-droplets or double cones among them as there are in their respective marsupial and lacertilian forebears? We cannot answer positively any of these questions or others like them; but every one of them is absorbing to anyone who is both interested in color vision and convinced of the past occurrence of cone-to-rod and rod-to-cone conversions.

Withal, the very existence of any capacity for hue-discrimination has been proven for so very few groups—none of them anywhere near the direct road of primate evolution—that much pioneering work remains to be done before anyone need concern himself with 'systems' and their phylogenetic significance or lack of it. It would be very fine if a moratorium on new genetic theories of color vision could be enforced, until a great many more cold facts have been garnered.

Evidence for Color Vision—The techniques, some of them very ingenious and some of them very stupid, which have been used to ascertain whether particular animals discriminate hues, defy classification. All of them however involve an all-important potential pitfall which at first went unrecognized, was later disposed of most inadequately by one means or another, and nowadays constitutes the careful investigator's most time-consuming concern. This pitfall is the danger of concluding that the animal has discriminated between two color-stimuli on the qualitative basis of hue, when he has actually discriminated them on the quan-

titative basis of brightness. Nor may it be forgotten that two stimuli, which differ for us in hue and in brightness, may be alike in both hue and brightness for an animal, and still be distinguishable by him upon yet another basis—saturation. It is on this basis, be it remembered, that the dichromatic human distinguishes two 'yellows' which to the normal appear respectively red and green.

There is a certain amount of purely observational evidence for color vision in some groups of vertebrates which, though it is no proof, is strongly suggestive and did seem evidence enough to the elder school of naturalists. Animals, particularly diurnal ones, are often brightly colored; and there are often sexual differences which are either permanent or nuptial—associated with the breeding season—as in some fishes, salamanders, lizards, and birds. Where the coloration is sexual, it is easy to assume that it means color vision on the part of the opposite sex at least. Indeed, this assumption was the very basis of Darwin's theory of sexual selection. Where gaudy colors are not obviously involved in sexual recognition one may assume that they indicate color vision on the part of the animal's natural enemies—particularly where we can be at all sure of concealing' or 'advertising' colors. 'Protective coloration' fools humans, which it might not do if they were color-blind. It fools the animal's enemies as well; and so, runs the argument, the latter must have color vision, and moreover a system much like that of man. Color-changes to fit backgrounds, while not nearly so common or precise as once thought, could only mean the possession of color vision on the part of the changer. Albino and isabelline birds are noticed, ostracized, and killed by their normal relatives. Though this may imply only intensity-discrimination, the hoarding habits of magpies, bower-birds, and others indicate a fascination and æsthetic interest in color as well as brightness. Bulls were 'well known' (before the days of experimental psychology) to be angered by red objects. The mink is claimed by trappers to be very curious about anything red, and it has seemed only natural that animals should be able to distinguish at least this color, since spilled blood can be so important to them. Finally, the coats of nocturnal birds and mammals tend to be drab and dark. The tacit implication is that such colorations are primitive, and that diurnal species have become dressed more gaudily because somewhere there are eyes to be confused by, or to appreciate, the colors which disappear—for all eyes alike—by the light of the moon.

Observational evidence has been sufficient to fuel the fires of many an argument between anglers, convinced or unconvinced that the color of a

fly means something to a trout; but experimental evidence is more satisfying to the souls of scientists and—when it is sympathetically interpreted to them—of sportsmen as well. These worthies have suffered abundantly with the psychologist's disinclination to try to study trout in small experimental aquaria, and with his warnings to the angler against assuming that if a mud-minnow has demonstrable color vision, a trout must have it also.

In our consideration of experimental procedures and findings, it may be said at the outset that much of the scientific literature itself is largely or wholly worthless. Almost always this is owing to incaution regarding the big danger mentioned above. In the work of one prolific investigator —Carl von Hess—it is also the result of certain assumptions which no one before or since has deemed it at all wise to make. Even where the researcher has made only correct assumptions and has been fully awake to all possible errors of interpretation, he has not gotten far—no one could—if his method has made use only of unlearned and untrained responses by the animal. These can be valuable, but only methods involving the *training* of the animal can be very fruitful, or make possible anything like a complete analysis of a color-vision system.

If the animal is to be made 'positive' to one of two or more stimuli—in other words, trained to evidence a discrimination if he can make one —he must be capable of trial-and-error learning. The angler may be impatient with the scientist for spending his time with the wrong species; but the scientist is as often annoyed by the rigors of his code, which forbids him to use any methods but those he considers the best, for this often prevents him from working upon the very species about which he is most curious. For if an animal is very stupid, like an opossum or a guinea-pig, he might have flamboyant colors in his brain, yet we might not be sure that he had any. If, like a snake, he eats infrequently and responds to mild punishment for his errors by getting angry, sulky, or flighty, he may be both highly intelligent and richly color-perceptive; but we may not be able to help him to prove it by giving him a proper incentive to work to make discriminations. The animal must get the idea of what is expected of him, must be willing to work for frequent small rewards, and must be able to do the task involved in demonstrating a choice between stimuli to the experimenter.

A Sample Ideal Procedure for Investigation—The reader will understand better the difficulties involved in really good color-vision research, and will be able to see for himself the loopholes in some of the

reports digested below, if an ideal investigation is outlined in some detail:

You wish to discover whether woodchucks, say, have color vision. Secure your animals, young enough to tame readily, and get them thoroughly friendly and used to handling while building your apparatus. This must be installed in a quiet room, in uniform surroundings so that no noise, odors, or asymmetrical lighting can serve as cues or be disturbing to the animal. The apparatus will be essentially a long, horizontal Y-shaped box, big enough so that the animal can be introduced at the bottom of the Y behind an opaque door, which you can release at your pleasure to let him amble comfortably down the long leg of the box to the junction, there turning either to right or left into one of the wings of the Y. You must be able to tell, visually or otherwise, where he is at all times; but he must not be able to see you while he is in the apparatus, else you may inadvertently give him a cue by your position or expression. As he approaches the junction of the Y he sees lights there, one of which eventually comes to mean to him that he is to turn toward the side on which that light is presented—if he can learn that much, as a woodchuck certainly can. If he makes the proper turn—say, into the right wing—you release a barrier in that wing which allows him to get at a standard-sized small piece of some woodchuck candy or other, perhaps carrot. An identical reward is in the left wing of the box behind a similar barrier so that olfactory cues are balanced for the animal, but if he goes to the left you keep up the barrier and shortly return him to the starting point for his next trial.

You must not ask the animal to make an absolute reaction, only a relative one. Memory for absolute values is very faulty even for man. At the junction of the box there must be two stimuli side by side, both of which he can see clearly at all times—even after he has made his choice between them. One of them leads him to food, and is called the positive stimulus. If he turns toward the side where the other stimulus is, he gets no food by thus responding to the negative stimulus. The positive stimulus must not be varied in hue or intensity, for if he associates it with food he will probably become greatly upset and bewildered if it is altered in hue or brightness. It must, however, be changed in one way, *i. e.* as to the side on which it is presented in successive trials. Otherwise the animal will probably fall into a 'position habit', going always to the right or always to the left, having really formed the association 'right = food' or 'left = food' instead of the one—'blue = food', say—you want him to establish. So, the blue stimulus must be on the right and on the left equal

numbers of times in the long run, but the alternation must not be at all regular or the animal will probably catch on to *that*. Some investigators, using choice-boxes for any sort of comparative psychological work, flip a coin before each trial to decide which side the positive stimulus is to have. In the course of a long experiment—and they are always long—there will be equal numbers of heads and tails.

When the animal has done his daily stint in trials—maybe ten, maybe a hundred, depending upon his capacity for work and the speed with which he gets filled up on the amounts of food which are big enough to interest him as rewards, you let him finish his dinner in his cage in the next room, and start with the next animal. The animals will get no more food until the next day's experimental period, ensuring that they will then be hungry and willing to work. Perhaps the food drive will not prove sufficient, and you may have to wire the floor of the choice-box so that you can give the woodchuck a light shock if he turns to the wrong side. The stimulus with which you shock him will now be the positive stimulus, and must not be varied; for he will now be making the association 'not blue = pain'. If you assume that he associated 'blue = safety', and change the other stimulus, he may seem to be unable to discriminate between the two, simply because he no longer knows what to avoid. Obviously, you must not both reward him for going to one stimulus and punish him for going to the other, or you cannot alter either and therefore cannot find out whether they can be made to look alike to him without looking alike to you.

The stimuli themselves may be squares of colored paper or they may be patches of light cast on ground-glass screens from behind. If they are of paper, you can have the advantage of working with fully light-adapted animals, but it will be harder to make certain that the discrimination is not on a basis of brightness alone. If they are lights, the room will need to be darkened. They may be colored by being passed through gelatine, glass, or liquid filters; or they may be more nearly monchromatic lights selected by slits from a broad, bright spectrum. In any case no wavelengths present in one should also be present in the other. It must be convenient to alter their intensity over a great range without changing their hue, though of course only one will be so altered in any given course of training. This will require changing the distance of the lights from the screens, or interposing various thicknesses of ground glass or smoked wedges which do not change the size or shape of the stimulus-patches.

Suppose the woodchuck has learned perfectly to go always to the blue member of a blue-red pair of stimuli. You may now begin changing the red stimulus in brightness, to look for a point at which the two stimuli are equally bright to the animal. There is sure to be such a value of intensity of the red light, but if you are fortunate you will not identify it. If the animal has been discriminating the colors as such, he will continue to go to the blue no matter how the red may be altered bit by bit, trial by trial or day by day, up or down, in intensity. If on the contrary he has been going to the blue only because it was brighter, say, than the red for his eye (it matters not that the two may originally have seemed equally bright to your own eyes), then at some intensity value of the red stimulus he will break down and make chance scores—that is, go as often to one stimulus as to the other. On the face of things this will indicate that he is totally color-blind; but he may only have been paying more attention to the greater brightness of the blue than to its coloredness. In this case he will soon make the 'blue = food' association once more, even with the red stimulus held constant at the confusing value. But if he continues indefinitely to make chance scores, and goes to the *red* stimulus when this is brighter for him than the blue (the 'step-wise phenomenon'—always going to the brighter, or less bright, of any two stimuli), then he surely has no color-discriminatory capacity whatever.

If the two stimuli first used were not from near the opposite ends of the spectrum, however, the animal might break down at particular intensity-values, and still have color vision, of a different character from the normal human. Yellow and orange, or blue and violet, would probably look alike in hue to an animal with a dichromatic system anything like that of a 'color-blind' human (see pp. 97-9), whereas either member of one pair would always be discriminable from either member of the other pair, since the two pairs are on opposite sides of any possible dichromate neutral point. Where there is any suspicion that the species in hand is dichromatic, a search must be made for a neutral point or band—a spectral region which the animal cannot distinguish from a white light. But it so happens that no vertebrate species (unless it be the cebus monkey—see p. 516) has yet been found to have a dichromatic system, though unfortunately few investigators have so devised their experiments as to disclose dichromasy even if it were possessed by their particular animals.

If colored papers or objects are used, it is most convenient to eliminate the possibility of a brightness-basis for the discriminations by training the

animal to a color versus a medium gray, substituting other grays from a finely-graded series after the animal has become thoroughly trained to the color. If no gray elicits confusion between it and the positive stimulus, then the latter is being seen qualitatively. Several publishers here and abroad offer long series of colored papers, and gray ones ranging from pure white to dead black. In some of these gray series, no two adjacent samples can be told apart by the human, and it is not likely that many animals (except birds) have any finer capacity for brightness discriminations. Some of your critics, even so, are sure to say that if you had used more shades of gray, one of them would have confused the woodchuck which, you insist, can see blue. To silence all critics, one simply must use colored lights, whose intensities can be very gradually regulated. It will help though, if you establish that a woodchuck trained positive to a medium gray cannot identify it alongside of neighboring shades of gray.

Having established that your animals distinguish the hues of red and blue, you have made but a bare beginning. You now re-train them to other pairs of colors and try to find out how many hues they can discriminate as compared with man's 160 or so. By training to darkness versus a red wavelength, and increasing that wavelength slowly, the limit of the animal's spectrum can be found at that wavelength which, however intense physically, is invisible—at the border of woodchuck infrared. So, also, the violet spectral limit can be located. In the woodchuck, it will not be as low a wavelength as that of man, because of the strongly yellow coloration of the lens of the animal. Systematic pursuit between the animal's spectral limits, using pairs of wavelengths which are fairly close together in the spectrum, with the negative hue (after training) being gradually approximated to the positive one, will enable you to plot a graph of the rate-of-change-of-hue against wavelength. Comparison of this with the human curve will be interesting, and may be extremely valuable to color-vision theories and theorists. Similar examinations of a series of red-blue mixtures will disclose whether the color circle is closed by purples for the woodchuck, as it is for man. Perhaps you will find it possible to detect chromatic after-imagery in the woodchuck—by training him positive to blue-green, for instance, then seeing whether he gives the positive reaction to a neutral gray after being fatigued with red. And of course you will wish to determine his brightness-threshold for various colors, and to ascertain how color equations hold for him—what mixture of red and green looks the same to him as a given orange, what mixtures

are complementary for him, and so on. The animal's threshold of brightness-difference will be nice to know—indeed, this value, determined with white lights, might be worth doing first of all, for it will give you an idea as to how much you dare change, at one step, the intensity of a negative stimulus with which you are trying to confuse the animal in your search for hue-discriminatory capacity.

Now, no one has done all of these things with any vertebrate species other than *Homo sapiens* himself. Even if all of the really careful work that has been done, on all vertebrates, had been done on some one species, we would not know quite all of these things about that one animal. Far from being able to compare color-vision systems, all we now know positively—from well-conceived experimentation—is that a few animals do see colors and that a few others do not, and that apparently the color-seeing forms all have a mechanism much like our own. Obviously very, very much remains to be done!

In the following review of the experimental literature, the fishes are dealt with fairly completely—not because their color vision is any more interesting than that of other groups, but because it is better known and more different investigators have applied more different methods, with more different advantages and faults of technique and interpretation, to its study. The procedures and results with higher vertebrates are described more sketchily, since after having a given procedure once characterized for him, the reader can be spared any detailed reiterations of favorable and unfavorable criticisms.

Fishes—The reader's suspense, if any, may as well be relieved at once by the flat, if somewhat back-handed, statement that no fish is known *not* to have color vision. But the angler can take little comfort from the fact. As will appear shortly, he cannot predict whether a red fly will attract or violently repel the fish he is after. In fact, there is every reason to think that a dry fly, or a floating plug of any color, is seen by the fish merely as a dark silhouette whose form is much more important than its hue. Much though we may know of the color vision of laboratory fishes, and infer as to the color vision of game species, when it comes to wet flies and plugs the old rule still holds: what they'll take, they take, and what they won't, they don't.

The first scientific work on fish color vision was reported by Graber in 1884 and 1885. He made use only of untrained responses made by the fish toward different stimuli presented in pairs—the so-called color-preference technique. Working with the freshwater *Barbatula barbatula* and

Alburnus alburnus, later with the marine *Spinachia spinachia* and *Syngnathus acus,* Graber found a preference for darkness as opposed to white light, and a decided preference for red light over blue, produced by glass filters. Equating the colored lights in brightness for his own eyes (and of course assuming that they were then of equal brightness to the fishes), he determined that the animals preferred red to green, and went to green or blue when either was paired with a blue + ultra-violet (by which is meant, here and elsewhere in this discussion, *human* ultra-violet —that is, wavelengths beyond the short-wave end of the human visible spectrum. What is truly 'ultra-violet' for an animal may commence at a longer or shorter wavelength than the one which is just visible to man). By making a red light twenty times as intense as a blue one, Graber could force his fishes to show a preference for the blue.

The earliest use of the method of training seems to have been that of Zolotnitzky who, in 1901, fed fishes for a time on red midge larvæ and then attempted to deceive them with bits of colored yarn glued to a card which was held against the glass side of the aquarium. The fishes tried to get at the red pieces, ignored those of other colors. A first attempt to eliminate the possibility of discrimination on a basis of brightness-difference was made five years later by Washburn and Bentley, who induced a 'red=food' association in *Semotilus atromaculatus* by feeding from a red-marked forceps presented simultaneously with an empty green one. The dace continued to go to the red forceps even when it contained no food, and even when the shade of red was changed considerably in either direction of brightness.

In 1908, Reighard concluded that *Lutianus griseus* discriminates hues as such, for he failed to find what has since come to be called the stepwise phenomenon. Offering both red and blue baits to wild gray snappers in the open sea, he found that they avoided the red ones. They also preferred white to blue. Back in the laboratory, Reighard found that the brightnesses of the stimuli he had used were in the order white→red→blue. Since the fishes preferred the brighter member of one combination (white-blue) and the duller member of another (blue-red), he concluded that they were guided by color rather than by brightness. He was further convinced of this when he found that fishes negative to red baits refused all shades of red, at the same time accepting other colors which must have been matched in brightness for them by one shade or another of red.

From 1909 to 1915, a flood of papers appeared in which the capacity of fishes for hue-discrimination was debated pro and con, with Hess tak-

ing the negative side and with first Bauer, later Karl von Frisch, championing the positive. The influence of Carl von Hess can hardly be exaggerated, for he devised some ingenious procedures, and helped his critics to improve their own work by his continual insistence that the brightness factor was not properly controlled in previous and contemporary work. He himself tended to avoid the use of techniques in which any control of brightness was theoretically necessary. Some of his assumptions and interpretations were so repugnant to others, however, that his work served to stimulate an outpouring of research which might not otherwise have been done even yet. Being a very great physiologist, Hess made very great mistakes when he made any at all; and other investigators were quick to point them out.

Hess used two methods particularly: that of preference, and the study of the pupil-contracting effects of the colors of lights. His argument was as follows: The totally color-blind human eye and the dark-adapted normal eye (which is color-blind) see the green region of the spectrum as brightest, whereas to the normal light-adapted eye the yellow region of the solar spectrum is most luminous. This shift in the position of the peak of maximal brightness is of course the Purkinje shift (Fig. 30, p. 87), and is accompanied by a relative decrease in the brightness of red and a relative increase in the brightness of blue stimuli on passing from full light-adaptation toward dark-adaptation, upon reducing the intensity of illumination. If for fishes (or other vertebrates—or invertebrates!) the brightest spectral region is the green when they are *light*-adapted, and if they show no Purkinje phenomenon, then they are color-blind. If their pupils close further in response to green light than to other colored lights of equal physical energy-content, then the green is brightest for them, and they are therefore totally color-blind. Hess applied this argument not only to fishes but to a host of other animals as well.

The fallacies inherent in this argument are glaring ones, and the most important of them have been repeatedly explained by others. There is no justification whatever for assuming that the curves of spectral luminosity, with or without color-vision, must be the same for any animal as for the human. The writer would go even further, and insist that an animal could have color vision and yet have no Purkinje phenomenon—the latter exists at all, in man or animals, as a sheer fortuity: the peaks of absorption of the rod and cone photosensitive substances are not identical in location in the spectrum. If they were identical (and they might just as well be), there would be no Purkinje shift. The scotopic absorp-

tion maximum of a fish may be at a wavelength as high as 545 mμ, as contrasted with the human value of about 510mμ. Should the photopic maximum of the same fish happen to fall at the human value of λ557mμ (and it probably would) the Purkinje shift would be only 12mμ instead of 47mμ; and a downward shift of the photopic maximum could even bring the two peaks into coincidence. Too, the normal human retina is totally color-blind in the extreme periphery, yet even here the brightness values of chromatic stimuli are those characteristic of photopic, not of scotopic, vision. Thus a Purkinje phenomenon occurs here in the absence of color-vision. Human dichromates experience an inversion of the relative brightnesses of red and green, upon a change of adaptation—yet red and green, for them, are the same hue. They thus have an 'isochromatic' Purkinje phenomenon as compared with the 'heterochromatic' one of the normal trichromatic individual.

The argument from pupilloscopic findings is even shakier; for while in man the pupil is controlled reflexly from the retina and appears to respond maximally to a given color because that color is consciously seen as brightest, in the fish any iris muscles are entirely autonomous and there is no reason to suppose that the wavelength which most stimulates them will also maximally stimulate one or both sets of visual cells in the retina. The teleost pupil moves but little at best, and in his examinations Hess made no attempt to eliminate the passive effects of lens movements upon its size.

Hess worked largely with very young fishes, apparently in order to be able to have large numbers (up to 60) in the same small tank, so that their distribution in the spectrum thrown in the water would be devoid of crowding-effects, and would also be statistically significant. For this he has been taken severely to task, as also for making too few control tests with thoroughly light-adapted specimens, for disturbing these before testing by carrying them for some distance to a darkroom, and for ignoring certain performances when they failed to confirm his ideas.

With species after species, Hess found that the fry would usually gather in the green or yellow-green portion of the proffered spectrum (λ525-535mμ). He concluded that this region looked brightest to them, since he claimed that they were always step-wise in their preferences for white lights of different intensities. When pairs of spectral lights were offered, the choices of the animals determined a curve of relative brightness which simulated that of the scotopic human. Hess claimed to have eliminated the possibility that this was caused by a Purkinje effect, by

repeating the findings on light-adapted specimens. He also contended that the red end of the spectrum is shortened for all fishes (as for the scotopic normal, totally color-blind, or protanopic human eye). By driving the fishes toward the red end of a spectrum with an advancing shadow, he found that they would still congregate in the light when wavelengths as short as 620-640mμ were still shining on the aquarium; but when the shadow reached to λ650mμ they suddenly dispersed as if they were in complete darkness. When two lights were shone on the tank from opposite ends, their relative intensities could be adjusted so that the fishes swam indifferently through both colors of illumination. With this procedure Hess found that the green was brightest, that blue, yellow, and orange were less bright, and that red was darkest for the fish. The intensity of any color needed to 'balance' pure yellow was only half that required to balance green. Unlike Graber, he could make his fishes go to red, by making it far brighter than an alternative blue light.

Bauer worked with *Charax puntazzo* and *Atherina hepsetus,* to some extent also with a species of mullet, and a bit with *Box salpa.* He used filters of glass, gelatine, and paper and made a few experiments with spectral lights. He found that his fishes (except *Mugil*) were instinctively strongly negative to red (λ680-710mμ) and called this peculiar phenomenon 'Rotscheu' or red-fear, red-shyness. Reighard had observed it in *Lutianus* as noted above, without realizing of course how very many species would show it. Fishes generally seem either to shun red, or to prefer it decidedly. This paradox does not appear to have interested the investigators in this field; but, granting that the red is seen as such, red-shyness and red-love both seem to indicate a high attention-value for red. Though red is very common in the body colorations of fishes, it is probably rarely sufficiently illuminated to be seen as anything but black, for the red rays are the first visible ones to be eliminated as light passes down through water. Perhaps it is because red, distinctly visible *as* red, is so unfamiliar to fishes that it gives them such a start in one way or the other. Both the shunning and the pursuit of red may mean the same thing—that the fish sees the red vividly, that it is strange, and that it fascinates him. Young fish, to which everything is new and strange, seldom exhibit red-shyness; and even old fish may get over it in a short time.

Bauer also established that his fishes were quite indifferent to wide variations in the intensity of white light. He could not get them to settle down in either of any two intensities. Yet when offered red and blue they would go to the blue, and no juggling of the intensities of the two colors

would bring about an equal distribution of the animals. These findings were directly contradictory to those of Hess, irrespective of any difference of interpretation; for Hess had claimed that an intense red and a blue were responded to alike and perceived alike, and that *Atherina hepsetus* responded differently to white lights differing as little as by a 1 : 1.23 ratio in brightness. Later work by others has substantiated Bauer's contention that the intensity-discrimination of fishes is extremely poor. Of course, it is probably mostly a matter of attention-value, the intelligence of the fish not being up to par with its sensations.

Bauer's animals were, it is to be noted, thoroughly light-adapted. Dark-adapted specimens showed no red-shyness, and would freely enter red or orange illuminations (λ620-630mμ) which, when they were light-adapted, would frighten them over to the dark side of the choice-box. No such behavior was noted toward any intensities of white light except very high ones. Far from being blind to red as Hess claimed, the animals perceived it very vividly according to Bauer. When dark-adapted, they preferred red to a blue which Bauer considered to be of the same intensity. Therefore, he thought, the chroma disappeared from the red wavelengths sooner than it would for the dark-adapted or dark-adapting human. Both a photochromatic interval for red, and a Purkinje phenomenon, seemed to have been established for the species.

When spectral lights were used, the fishes did not prefer the yellow-green as Hess had claimed, but went to either yellow or blue-green. It is interesting to note that the photopic human has a secondary maximum of brightness in the blue region (unless the macular pigment happens to be excessive). The two maxima are perhaps more nearly equal in brightness for Bauer's species.

When the wavelength of a spectral light was moved gradually up from the violet end, the fishes first made definitely negative responses at λ510-mμ, and under a red filter (λ680-710mμ) they would scatter into dark corners if light-adapted, gather under the filter only if dark-adapted so that its redness was not apparent to them. This seems further evidence for a photochromatic interval for red (which does not occur in man), though no one seems to have pointed it out.

Mugil, being positively phototropic and lacking in red-shyness, lent itself to certain experiments impossible or inconvenient with the other species. Bauer paired a green light with a blue one and regulated their intensities so that the fishes gathered in the green. When both lights were reduced equally in intensity the animals shifted over into the blue

light, thus further demonstrating, to Bauer's satisfaction, a Purkinje phenomenon.

Box salpa preferred light coming through blue glass + frosted glass to that transmitted by frosted glass alone. Bauer concluded that this response was to hue as such, since the blue light was certainly the dimmer of the two and *Box salpa* is strongly positive to light. If it were responding to brightness rather than to color, the fish would surely have gone to the white light instead of to the blue.

Hess came forward with an explanation of Bauer's apparent demonstration of a Purkinje phenomenon in fishes. He argued that in the light-adapted fish the expanded retinal pigment would constitute a yellow filter, reducing the brightness of blue stimuli relative to long-wave ones. He found that a blue light had to be made four times as intense to balance a yellowish-red light for a photopic fish as for a scotopic one, and in experiments with light-adapted tiny carp he had to raise the intensity of a blue light six- or eight-fold to keep the fishes evenly distributed through it and a red which balanced the lower blue for the dark-adapted fish.

While no more conclusive-looking demonstration of the Purkinje phenomenon has ever been made, Hess concluded that it was not that dark-adaptation increased the brightness of blue and decreased the brightness of red—the true Purkinje phenomenon—but rather that light-adaptation left the brightness of long-wave stimuli unchanged and pulled down the brightness of short-wave ones. Some such effect may indeed occur along with the Purkinje changes, if the retinal fuscin actually does have any peak of absorption at all (which has yet to be demonstrated), and moreover has it in the short-wave end of the spectrum. But any such phenomenon is rendered very improbable by the recent demonstration that blue and red values are not altered for dark-adapted fishes whose retinal pigment has been artificially expanded with adrenalin (*v. i.*).

Hess denied the existence of red-shyness, or at least that it indicated color-vision; but he failed to look for it in specimens which would be most likely to show it—mature, light-adapted fish of negatively phototropic species. His finding that red and blue lights could be so balanced that a light-adapted fish would show no preference for either—even supposing that others had found the same thing, which they have not—might only mean that the fish had had opportunity to become accustomed to the red and recover from its red-shyness; he does not give the time-periods involved. Where Hess finds that a fish will leave a blue and go to a bright red, he may have been dealing with a red-loving fish—he does

not mention the species by name. And, where he finds that the fishes scatter when the spectrum thrown upon them is progressively narrowed down to red alone, it might only mean that the animals were avoiding the red because it was such a strong stimulus to them and they were left with no other light in which to congregate. Hess believed, on the other hand, that in reduced illuminations blue lights became too strong for the fish owing to the retraction of the retinal pigment, and in this way explained Bauer's results with red-blue pairs, wherein the fish would enter the red light only when the intensities of both were lowered. For Bauer, this meant that since the fish had become dark-adapted it could no longer discriminate hues, and consequently had no redness to avoid; but to Hess it indicated that the blue light had become unpleasantly bright, and was seen achromatically just as in light-adaptation, but with far greater brilliance because of the removal of the shielding pigment from its pathway.

It is interesting to note that in fishes the migration of the pigment itself, and of the cones, has recently been shown to take place maximally in yellow light when physical intensities are equated. Red and blue evoke the least movement of the elements, with orange, yellow-green, and blue-green intermediate in effectiveness. This checks with Bauer's demonstration of a subjective brightness-maximum in the yellow, and also with the peak of absorption of the photosensitive substance which von Studnitz claims to have extracted from fish cones.

Von Frisch emphasized two techniques, one of which involved training the fish to respond positively to one of two stimuli regardless of what the other one might be, and the other of which made use of the response of the skin pigment cells to colored backgrounds, which since the work of Pouchet in 1876 had been known to be mediated through the eyes (see next section). Frisch's training technique was essentially the one which he had applied so successfully to the bee, in another controversy with Hess which lies outside the scope of this treatment. After the fish had been trained to come to a certain colored tube for food, regardless of where that tube might be in a series of gray tubes in the aquarium, he omitted the food (thus controlling olfactory and gustatory cues) and found that the fishes—'Ellritze' (*Phoxinus lævis*)—always went to the colored tube though six gray tubes at a time, out of a total of 50 gray shades ranging from white to black, were presented along with the color. Since there was no shade of gray which the fishes mistook for the training color, Frisch concluded that they could discriminate hues.

In this same way Frisch also determined the discriminability of colors from each other, and found that the fishes confused red with yellow, but not blue with green or either blue or green with either red or yellow. Purple was also sometimes confused with red and yellow, suggesting a closed color circle which was firmly established years later for *Phoxinus* by other investigators employing spectral lights. In 1923, Burkamp offered *Phoxinus* as many as 23 pigmentary grays simultaneously with a training color, whose position in the mosaic of grays was irregularly varied, and found that the color was never confused with any gray—an abundant substantiation of Frisch's earlier work.

Frisch essentially repeated Zolotnitzky's experiments, which Hess had also repeated (with altered technique and complete failure). After training Ellritze on yellow meat, Frisch substituted bits of yellow paper on gray backgrounds of the same texture, including a shade of gray which matched the yellow for his own dark-adapted eye. On each gray background he also fastened bits of other gray papers both lighter and darker than the yellow. Trained fishes snapped mostly at the yellow bits, untrained ones equally at all three. Hess repeated this experiment also, again altering the technique, and got negative results. His fishes trained positive to yellow would afterwards snap at blue objects as often as at yellow ones; but it has been pointed out that he had not kept blue objects out of the situation during the training, and had made no effort to prevent any 'blue = food' association at the same time that he was building up the 'yellow = food' one. Frisch also turned the weapon of retinal migration back upon Hess, when he eventually demonstrated that the particular intensity in which *Phoxinus* ceases to discern the chroma red—is dark-adapted, in other words—is one in which the photomechanical changes will run to completion of the dark-adapted pattern (see p. 149).

The response-to-background technique also yielded positive results on *Phoxinus* in Frisch's hands; and since he first popularized the method it has since, on less drab species, yielded even more striking findings than his own. *Phoxinus* ordinarily responds to a yellow (or red) background by becoming yellowish. It has no other capacity for color change; but it responds to light and dark backgrounds by corresponding lightenings and darkenings of the skin. Frisch took advantage of the fact that the change in tone takes place in a few seconds, while several hours are required for the change in hue to be accomplished. From a finely graded series of black-gray-white papers, he was able to select a gray to which the fish made the same brightness-response as to a particular yellow paper.

By alternating the gray and yellow backgrounds he could thus keep the fish at a constant brightness of skin pattern. Left on the yellow background for an hour or more, the fish turned yellowish; but it would never do this on the matched gray.

Similar results were obtained with *Crenilabrus pavo* and *Trigla corax.* And, when yellow and blue fluids, both so concentrated as to appear black, were used as backgrounds, Frisch found that gradual dilution evoked graded brightnesses of skin coloration but an expansion of the yellow chromatophores occurred only in the case of the yellow solution. He chose two shades of yellow papers and found a gray which gave the same brightness-stimulation as the lighter of the yellows. When the skin of a fish had adapted to the darker yellow, substitution of the gray for the dark yellow caused an immediate paling of the skin. This demonstrated that the two yellows differed more in brightness than did the lighter yellow and the gray. Prolonged exposure to either yellow now caused a yellowing, which would not take place on the gray, or on green, blue, or violet backgrounds—on these, the xanthophores contracted.

Freytag shortly repeated some of Frisch's work with *Phoxinus* and got negative results. His fishes responded to the shade of the background but not to the color, even after twenty-four hours. Reeves later rather lamely suggested that Freytag had not waited long enough for the color change to take place. It is far more likely that Freytag's specimens simply came from the wrong river! At about the same time, Haempel and Kolmer were reporting their work on *Phoxinus lævis* and *Cottus gobio,* where the only color-mimicry they observed was a reddish response of *Phoxinus* to red backgrounds, no reaction being given to gray, or to other colors. Their specimens had come from a red-bottomed river, the Würm. Years later, in 1920, Schnurmann found that while Munich specimens behaved just as Frisch had described them, others from Ulmar gave no color-response to yellow, orange, or red backgrounds.

Another fish which is a favorite with physiologists is our own killifish, *Fundulus heteroclitus;* but unfortunately its dermal color-repertoire is as limited as that of *Phoxinus.* Connolly placed killifishes on backgrounds illuminated with spectral lights carefully equated in intensity by thermopile measurements. It took several days for the specimens on red and yellow grounds to become distinct from those on blue. A more versatile species was found by Frisch—*Crenilabrus roissali,* which adapts to red, green, and blue grounds as well as to yellow ones. To the achromatic (scotopic) human eye the brightnesses of the backgrounds offered by

Frisch were in the order yellow→green→blue→red. Since the fish reacted to the 'brightest' color by contraction, to the 'darkest' color by expansion of its pigment cells—this being quite unorthodox for pigment cells to do —Frisch concluded that the reactions were being made to the hues *per se.*

Critics were quick to point out that while these reactions admittedly might be made to the hue of the background, and mediated through the eyes (several investigators had been so thorough as to make sure that that blinded fishes could not make them), there was still no reason to assume that the fish must therefore be consciously aware of the hues. These objectors were largely silenced by the work of two American investigators, Sumner and Mast.

Sumner, in 1911, had been intrigued by the rapidity of the color changes of flat-fishes as they glided over the changing bottom. In *Rhomboidichthys podas, Rhombus lævis,* and *Lophopsetta aquosa,* he had demonstrated dermal responses to shade, color, and pattern. These species reacted to black, brown, and gray, but not to red or yellow. A few years later Mast published his classical studies on two other genera, *Paralichthys* and *Ancyclopsetta,* which in a startling way mimic blue, green, yellow, orange, pink, and brown. Shade, color, and pattern are all closely followed by the dermal adaptations.

Mast painted the floors of a number of tanks, some with a single color and others with two colors on the respective halves. He allowed flounders to remain on single colors for six weeks, then placed each fish on the dividing line of a bicolor tank floor. Blue-adapted fish swam at once to the blue side of a two-color tank 88% of the time, green-adapted fish 70% to the green side. But red-adapted individuals turned toward the red only 26% of the time. If their choice had been a 50:50 one, Mast contended, it would have meant that they could not discriminate the red hue from the other. 26% meant actual avoidance of red. When the other side of the tank happened to be blue, red-adapted flounders went to the red side only five times, to the blue 115 times!

The responses of Mast's flounders were so immediate, so obviously visual, that they were far more important than the *Phoxinus* work as grist to the mill of the proponents of piscine hue-discrimination. But brightness was not controlled, nor was a series of confusion-grays employed in Mast's experiments. They demonstrated color-discrimination, but did they show *hue*-discrimination? By this time most of those interested were convinced either that Hess or Frisch was right; but some remained unsatisfied with the results and the limitations of colored-

paper techniques. Sporadic investigation continued, with training methods and filtered or spectral lights emphasized more and more.

Goldsmith came to the support of Frisch with a report on *Gobius fluviatilis* and *Gasterosteus aculeatus*. The former of these species was red-shy, the latter red-loving, as were also some young plaice which she tested. Goldsmith's experimental results were practically worthless, for in an attempt to prove hue-discrimination she fell into the brightness trap in a new way: where so many others had assumed that equal brightnesses for the human would be equal for the fish, Goldsmith assumed that equal energies would be equally bright. That idea was alright for its time; but she proceeded to equate the energies of her lights by adjusting their intensities until they darkened photographic plates to the same extent in the same exposure time. The visible spectrum of any camera film is of course very different from that of any eye. With such stimuli, Goldsmith established that *Gasterosteus* preferred red→yellow→green→blue, and concluded that the choices were made on a basis of hue. Her one permanent contribution was in finding that a fish trained to come for food to colored forceps would persist in examining empty forceps bearing the training color for as long as four days after a previous test.

No new reports appeared until just after World War I, when those of White and Reeves—the latter perhaps the most important single contribution to date—were published. White worked on *Umbra limi* and *Eucalia inconstans,* using pigmentary colors. She found that grays and white lights were scarcely discriminated as to intensity, and that after training to one of two colors neither species could be confused by any intensity of the negative stimulus. *Umbra* discriminated between red and green, red and blue, and yellow and green. *Eucalia* could discriminate red from green, but not blue from yellow. White's steps in albedo were coarse, but she reasoned that since the discrimination of intensity was so poor there was no need of seeking any more perfect match in brightness than the fish was able to make. Criticized on this ground, she repeated her work (as Hineline, 1927) but with a technique actually inferior to her original one. Misled like Goldsmith by a prevalent notion that equal energies should arouse equal subjective brightnesses in any and all animals, she obtained filters equated within a few per cent in total visible energy transmitted. With these, she found that *Umbra* was able to discriminate red (λ660-700mμ) from green (λ510-550mμ), red from blue (λ400-450mμ), red from yellow (λ560-600mμ) and (with difficulty) yellow from blue, but could probably not distinguish blue

from green (λ510-550mμ). One member of each pair was the positive stimulus at first, and the fish was later retrained to the other stimulus—a further attempt to eliminate preferences or any possible discrimination on a brightness basis.

White-Hineline's decidedly inconclusive work was far overshadowed by the restricted but thorough and beautifully controlled investigations of Reeves, a student of Reighard. Reeves was content to employ two hues only, devoting her time and energy entirely to the elimination of the brightness factor from this one discrimination. While other more recent researches have yielded superficial information about much more of the whole color-vision system of the fish, that of Reeves stands as a model demonstration of an unquestionable discrimination of hue *as* hue.

She used an adaptation of the Yerkes-Watson discrimination box described in the 'ideal investigation' outlined above, and studied the untrained and trained responses of several species, chiefly *Semotilus atromaculatus* and *Lepomis gibbosus,* to white and (filtered) red and blue lights. The blue filter passed the short-wave end of the spectrum up to λ509mμ. Several different red filters were used, principally one which transmitted only wavelengths longer than 589mμ.

The dace (*Semotilus*) showed very poor brightness-discrimination in preliminary experiments. At least they *would* not distinguish intensities which differed in less than 1:4 ratio. When two such intensities were presented, apparently barely discriminable by the animal, the insertion of the red filter in the path of the brighter light (without any other change being made) produced a marked change in behavior, although the intensities were presumably no longer discriminable, being too nearly equal. The fish evinced a strong red-shyness, which however was temporary and in young individuals was absent. Dace were now trained positive to a dim blue stimulus versus an intense red one. After training, the intensity of the red was cut to 60%, 37%, then 20% of its original value, the dace still going to the blue to seek food 90% of the time. Repeated with more gradual reduction, the typical response was an 85%-95% correct choice until a critical value of red intensity was reached, at which the accuracy suddenly dropped to 60%!

At this point, the two stimuli were obviously alike in some way for the fish. A permanent performance of 50% or 60% accuracy would have meant that they were wholly identical; but Reeves found that with no further changes the accuracy eventually rose again to 83%, and upon a still further dimming of the negative stimulus the performance went

still higher and remained high. She felt justified in concluding that the intensity of red at which confusion at first occurred was one at which the brightnesses of the red and blue lights were equated for the dace, and that the confusion was due to a re-learning, the fish switching its attention from the brightnesses to the hues and making the association 'blue = food' which she had supposed to have been made in the first place. Another dace showed no such temporary confusion at any intensity of the red, indicating that it had been attending to hue from the first, rather than to brightness. Of course there were two other possibilities—that the fish, from the outset, were not going to blue so much as avoiding red, with individual differences in this red-avoidance; or, that the confusion was due to getting used to red and ceasing to avoid it, the 'blue = food' association being not yet established. But, interpreted in any of these ways, the experiment had demonstrated hue-discrimination, for there could be no redness-fear in the first place unless there were redness-perception.

The sunfish (*Lepomis*) proved to be more sensitive to intensity than the dace, tending to lurk and hide in dark corners rather than come out and face white lights to which the dace had readily gone. In keeping with this, Reeves found a greater capacity for discriminating intensities, the ratio needing to be but 1:2+, which however was still far short of the 1:1.23 difference claimed by Hess—and yet was far better than the capacity elicited from any other species by any other investigator before or since. When offered blue versus red, the sunfish was extremely slow to build up the 'blue = food' association; and again it was the larger specimen which showed red-shyness, the younger specimen lacking fear of red as also of many other things which would startle the older animal. After successful training positive to blue, the gradual dimming of the red stimulus to a certain value caused the same sudden confusion, at that critical intensity, which had been manifested by the dace—the intensity this time being, by coincidence certainly, the very one at which the red and blue were identical to Reeves' own dark-adapted eye (the fishes were *light*-adapted by an initial white illumination before each trial). The sunfish recovered from the confusion at matched brightnesses much quicker than had the dace, however. Both species readily discriminated the training-blue from 'gray' light (produced with several layers of photographic negatives as a filter) which matched it in brightness for the human; but they behaved very differently from what they did when a blue and a red, also of equal brightness to the human, were

simultaneously offered. Reeves drew the natural conclusion that the fishes saw the red and the gray as qualitatively different things, since the two equalled the same thing (the blue) for the human in brightness. There is an obvious fallacy here, but it is of no importance to the main conclusion that hue discrimination occurs in the two species.

Both species were much more sensitive to lights when dark-adapted, but Reeves could find no evidence that there was any change in the relative brightness of red and blue or of red and white. She therefore questioned the occurrence of a Purkinje phenomenon, though on quite different grounds from those of Hess. The importance of the presence or absence, or demonstrability, of a Purkinje shift for the certainty of hue discrimination has been greatly overemphasized as explained above (pp. 474-5).

Reeves came close to the conditioned reflex technique—a very modern tool of research on animal color-vision—in her observations on untrained mud-minnows (*Umbra limi*) and shiners (*Notropis cornutus*). She noticed that the respiratory rate of mud-minnows was the same (30/min.) in daylight, and in daylight plus tungsten-lamp illumination. When she slipped a ruby glass plate under the lamp the fishes settled to the bottom, had fits of trembling, and more than doubled their breathing rate. Shiners breathed 60 times per minute in diffuse daylight, 85 times per minute when a carbon filament lamp was turned on in addition, and 150 times per minute when a ruby filter was placed over the lamp. In this experiment it was perfectly clear that the response was to redness as such, since the respiration rose with an increase of brightness, but rose still higher when that brightness was somewhat reduced by a filter which introduced hue.

Untrained *Hyborhynchus notatus* would readily approach blue and gray patches of light equated in brightness for humans and offered side by side. But when a red, equated in brightness with the other two stimuli for the light-adapted human, was substituted for the gray, the minnows stayed away. Untrained *Semotilus* behaved identically. When, after the blue and red had been offered for two hours, the gray was returned in place of the red, they approached the patches promptly; but the red-shyness reappeared when, three hours later still, the red was once more exchanged for the gray. Strangely enough, trained dace were just as shy of gray as wild ones were of red.

Differential behavior of fishes toward blue, red, and gray matched in brightness for the human eye, either light- or dark-adapted, is suggestive

but not conclusive. Here again Reeves improperly assumed that lights equally bright for one animal would be equally bright for another, which could be true only if their spectral luminosity curves were completely superimposable or at least coincided with, or crossed, each other at the particular wavelengths used.

Since Reeves' time, all of the training experiments reported have been made on *Phoxinus lævis* and, to some extent, on *Gasterosteus aculeatus*. Schiemenz, Wolff, Kühn, and Hamburger, working from 1924 to 1926, are the last prominent names in the literature to date. Spectral lights were used almost exclusively, and the spectrum of the fish explored with sufficient thoroughness to establish its limits roughly and to yield curves of hue-discrimination—that is, graphs of the closeness of two just-discriminable wavelengths plotted against their position in the spectrum.

Light-adapted fishes were trained to jump for food held just above the water on glass rods bathed with narrow spectral bands. They would continue to seek food on empty rods in the training color even when twelve intensities of it were interchanged at random, and were never confused by any intensity of any other color except the training color's immediate neighbors in the color circle. Lights too low in intensity to be seen as colored by the human were the only ones confused by the fish. Trained to seek food in a particular colored area among others—a multiple version of Reeves' two-choice presentation—they were never confused by the other colors regardless of intensity-relationships. These species apparently give much more attention to hues than to brightnesses, in contrast to Reeves' material.

The animals' ability to discriminate hues close together in the spectrum was better in the short-wave end, a little poorer in the long-wave region, than that of man. They could be trained to ultraviolet as far as $\lambda 365 m\mu$; and this region, violet, blue, green, yellow, and red were all qualitatively different for the fish. When offered the whole spectrum on the wall of the aquarium, they gathered in the particular region to which they had been trained, and snapped the air seeking the accustomed food. If the spectrum was moved, the fishes shifted with it. If the intensity of the whole spectrum was lowered they still gathered in the training color as long as it had color for the human, despite repeated scattering by hand and shifts of the position of the spectrum. And they could not be trained at all to particular brightnesses of *white* light.

These high-school Ellritze thoroughly dispose of Hess's contention that all fish are color-blind. Although the English worker, Bull, has very

recently brought the conditioned-reflex method to bear upon the question of hue-discrimination in fishes, his revelation of the ease and speed with which simple discrimination can thus be proven, as compared with the training method, has come too late to save any investigator's time or trouble. Bull's methods cannot rival the training technique for the laborious working-out of a color-vision *system,* and it is this that remains to be done. No reasonable student of the problem any longer doubts that fishes—all duplex teleosts at least—can experience hue as a sensation-quality apart from brightness.

The 1924-1926 work discussed above has revealed some preliminary data on the nature of the hue system of *Phoxinus,* which has such a head start that probably no American species will be worked out sooner. Hungry, *partly* trained individuals have been found to snap for food in bands of wavelengths neighboring the ones used for training. Thus, red-trained animals will snap also at yellow while still incompletely trained, yellow-trained ones snap also at red and green, 'blue' animals at green and violet. Some of these confusions persist after thorough training, enabling the determination of a curve of hue-discrimination which is interestingly different from the human one, and has seeming maxima at λ430mμ, λ485mμ, λ590mμ, and probably at λ655mμ. The human is nowadays believed to have but two genuine maxima, at λ490mμ and λ580mμ, though from one to three other secondary maxima were described by the older investigators. Probably some of the 'maxima' of *Phoxinus* will disappear in future investigations.

A valuable finding upon imperfectly trained Ellritze was that those undergoing training to red made most of their erroneous snaps in the violet and ultraviolet, and vice versa. This demonstrates a recurrence of redness in the short-wave sensations, closing the color circle through the red-blue and red-violet mixtures which the human sees as the extra-spectral purples. It would be most interesting to know, though sadly unknowable, whether ultraviolet *is* 'red' to fishes that can see it, or would look red to us if our optic media did not fluoresce it so completely into pallid short-wave visible light. For many fishes, the penetrability of the ocular media ceases in the (human) violet; but in *Gasterosteus aculeatus,* for example, the wavelength 313mμ can reach the retina. Merker, the leading investigator of the biology of the ultraviolet, notes that these sticklebacks can be trained to snap for food in the wavelength band 313-253mμ, but thinks that in such very low wavelengths the food is seen as a shadow cast by visible light into which the fluorescence of the

water converts the extreme ultraviolet. The fixing of the short-wave limit of the true visible spectrum for such an animal is very difficult. In *Gasterosteus,* in contrast to the frog, no retinal action-current can be detected in ultraviolet illuminations; and yet a pure λ366mμ beam, apparently visible to the fish, causes the complete pattern of retinal photomechanical changes. Quinine-fluoresced light will do likewise, however. Through fluorescence, ultraviolet light may paradoxically lead to seeing without actually itself being seen. The exact position of this lower spectral limit for fishes in general is of little or no biological importance anyway, for a meter or less of water eliminates all of the ultraviolet in sunlight.

Something, then, is known of the spectral limits, hue-categories, and hue-discrimination in different spectral regions for these two fishes, and we can hope eventually to learn all about the system they employ—whether it has three component central processes, or more. We can already be certain that they are not dichromatic, for they distinguish too many hues and, according to Hamburger, get no sensation of 'white' from any monochromatic light, and therefore have no neutral point. Hamburger made a beginning at an analysis of the laws of color mixture as they apply to *Phoxinus.* He found that fishes trained to white light not only discriminated it qualitatively from every spectral region but recognized, as white, human complementary mixtures of yellow and blue, red and blue-green, orange and blue-violet, and so on. A similar demonstration of complementary colors for *Betta splendens,* by an entirely different technique, was incidental also to the work of Beniuc (see pp. 364-5).

It is one thing to be able to say that all cone-rich teleosts assuredly have color vision, and quite another thing to say how much color means to fishes. The environment of the average species is rather drab. We have seen that particular colors—red and blue—may provoke particular species to vigorous responses. Miss Reeves' fishes tended, however, to pay more attention to brightness than to hue. How successfully might *form* also compete with color for the attention of a fish? Is the shape of an artificial lure perhaps more important than its color, even though the latter is perceived? Recently some experiments have been made along this line by a Japanese, Horio:

This investigator trained carp positive to a red disc and negative to a blue one. They learned this discrimination readily—not so readily, however, the discrimination of a white triangle (positive) and a white square (negative). The better to compare the effectiveness of form and color,

Horio then sought a pair of colors which would be as difficult for the fish to tell apart as were the triangle and square. He found it, in violet and blue. Trained positive to a violet disc versus a blue one and to a white triangle versus a white square, then offered a violet square versus a blue triangle, the fish went to the positive color rather than to the positive form. Color thus seems to lie between brightness and form as regards its attention value.

When color and form were used in summation instead of at cross-purposes, Horio obtained some unexpected results. Fishes partially trained to a red or violet disc versus a blue one, and separately to a white triangle versus a white square, made more accurate choices when offered a red or violet triangle versus a blue square than when the stimuli differed in only color or form. But when these independent trainings to color and form were both complete, the fishes made more errors on the combination stimuli than on the simple ones. Horio decided that this must mean that the fishes had had time to develop 'red disc = food' and 'white square = no food' associations, not merely 'red = food' and 'square = no food' ones. Hence, the red triangle had a weaker effect on them than either the red disc or the white triangle.

Amphibians—Most of the Amphibia are nocturnal and secretive, and it is difficult to see what color vision could do for them if they had it. The common (ranid) frogs are arhythmic animals however, which might have, and might benefit from, color vision. Except for one recent Japanese report of work on a larval salamander, which the writer has not been able to see, all of the efforts to find color vision in amphibians have been made upon frogs.

As early as 1900 it was established by Himstedt and Nagel that the frog has a Purkinje phenomenon. Their technical tool was the electro-retinogram, the record of retinal action-currents. Granit and his co-workers, with similar but refined methods, have found the photopic and scotopic maximally-effective wavelengths to be practically the same (560mμ and 507mμ) as those giving the peak brightnesses for the human. Therman, in the same laboratory, found an increased electrical response in blue light and a decreased response to red, in dark-adaptation. Expansion of the retinal pigment in darkness by injections of adrenalin failed to upset this relationship, casting further doubt—if any were needed—upon Hess's interpretation of the Purkinje phenomenon in fishes.

The presence of a Purkinje phenomenon, however, is no evidence for color vision, but only demonstrates the presence of two types of receptors with different absorption spectra. A Purkinje phenomenon of the isochromatic type could exist in an animal with a duplex retina and achromatic vision. Hess even denied the existence of the phenomenon in the frog, on the basis of pupilloscopic findings, claiming the frog pupil to be most responsive to green light both scotopically and photopically. We have seen how devoid of any certain meaning such findings are, particularly when gained in an animal whose iris muscles are wholly or largely autonomous. Pupillometry is scarcely more trustworthy as a means of determining accurately the limits of the spectrum; but it is a convenient means, and with it Hess determined the spectral limits of the frog and other amphibians to be practically the same as those of man.

Nearly forty years ago, Yerkes studied the learning ability of the green frog (*Rana clamitans*) in very simple mazes, employing red and white cards as parts of the stimulus patterns offered the animal as cues to true path and blind alley. The frogs were guided partly by these grossly different visual stimuli; but neither Yerkes nor anyone else has since gone further than this in attempts to train frogs to discriminate hues. Their learning ability, which is next door to zero, makes this quite out of the question. Hess and others got nowhere with the color-preference method in frogs; and even the conditioned-reflex technique, which obviates any need of a conscious choice by the animal, gave no results when Bajandurow and Pegel tried to apply it to the frog in 1932.

Promising leads have come lately from the electroretinograms picked up from the excised eye under monochromatic stimulations. The Helsinki group found that the form of the gram is different for colored stimuli, when differences in intensity are ruled out. They have decided that there must be three systems in the frog eye:

A. The rods, with their rhodopsin.

B. Rods, or cones, containing a substance absorbing light maximally in the blue and violet ('green rods' [p. 58]? cone oil-droplets?).

C. Cones of at least two types (the singles and doubles?) overlapping with respect to the distribution of their sensitivities to spectral lights.

They conclude that "the selective effect of wavelength on the retina represents a mechanism that can be used for color differentiation." But when they plotted the spectral distribution of the effects of strong monochromatic lights upon the subsequent electrical response to stimulations

with a standard λ500μ source, they obtained a curve which coincided neither with the rod-spectrum nor with the cone-spectrum as deduced from the ordinary electroretinogram—nor with a curve representing the superposition or resultant of the two. This is rather indigestible, and it is to be hoped that these workers (now established in Stockholm) may soon decide to turn their recording apparatus upon some animal—*Phoxinus* for example—which is known to have color vision and whose system is susceptible of cognate studies with various other procedures.

The only investigator who, without 'hedging', makes an out-and-out claim of color vision for the frog is Birukow. In 1939 he reported experiments based upon an application of the optomotor reaction (pp. 301-2): In 1927, Schlieper had reported that when the alternate stripes on the revolving drum used for eliciting compensatory movements from the animal inside it were respectively colored and gray, there was always some shade of gray to be found which, paired with a given color, would evoke no response from the animal. The animal behaved as though the visual field had become homogeneous, its motion invisible to him—in other words, the animal acted as if it were color-blind, even though it belonged to a species known positively to have color vision. Schlieper used several diurnal insects, two fishes, and the lizard *Lacerta vivipara.* By all of these, the optomotor reaction was apparently given only to patterns of brightness differences, and Schlieper concluded that the critical shade of gray which, paired with a color, brought no response, must be a brightness match for that color.

Von Buddenbrock and Friedrich, a few years later, reasoned that if two colors were adjusted in brightness so that each by itself matched the same gray, the two colors would then be equal in brightness for the animal. Such matched colors, applied in alternate stripes to a drum, did effectively stimulate their animals to make compensatory eye movements. Unfortunately, they employed this technique only with invertebrate material—a species of crab.

Birukow was the first to use their procedure on vertebrates, and he chose to study *Rana temporaria.* At least, he assumed that Buddenbrock and Friedrich's ideas were correct, and was prepared to try them out on the frog. But he found that neither red nor blue could be 'matched' by a gray for this animal. Apparently the frog differed from the lizard in some way; and the failure to find a gray which, alternated with a color, suppressed the reaction, proved the perception of the color. Birukow could offer no explanation of Schlieper's results with the lizard, nor

could he very well apply Buddenbrock and Friedrich's principle of pairing off colors that matched the same gray. He did find that yellow-green and its spectral neighbors could be equated to grays, and decided that in the case of the frog (in contrast to the lizard) this meant that they *were* gray to the animal, yellow-green thus being a neutral point in his spectrum. At intensities below .04 lux, any color could be equated to a gray —this being the realm of pure rod activity. A marked Purkinje phenomenon was found, but above 30 lux there were no further changes in the relative brightnesses of different colors. When the drum was striped with alternate red and blue, and the stripes made progressively narrower, the reaction was inhibited when the visual angles subtended by the stripes were twice the threshold values for black and white stripes. Birukow concluded that the 'visual acuity for colors' was only half of that for black and white. Ignoring the fact that the differences in albedo of the adjacent stripes were far from the same in the two cases, he correlated these findings with the fact that the cone-to-rod ratio in the frog's area centralis is 1:2. Again, ignoring the fact that while rods may play no part in color vision, cones do play a part in black-and-white vision, he related his findings to the fact (earlier demonstrated by himself) that it is the rods rather than the cones which, in the frog, set the retinal limits of resolving power. From all this he drew confirmation that the rods play no part in color vision.

The use of the optomotor reaction as a means of studying animal visual acuity has been severely criticized. Apart from this however, does the frog's compensatory reaction to red and blue versus gray stripes of any and all albedos prove color vision? There is grave doubt of it. The average investigator, finding that he could obtain a yellow-gray match that abolished the reaction, would certainly not give up on red-gray combinations until he had tried many close grades of gray. And as a matter of fact, a close perusal of Birukow's report reveals that his animals did have matches of gray and blue, despite his conclusion drawn to the contrary.

Again, the reaction to blue versus red of any and all albedos could have a purely physical basis. Considering such factors as chromatic aberration, it is hard to imagine how the parade of contours between the red and blue stripes could be made to disappear even for a totally color-blind animal for whom the red and blue were exactly matched in brightness. The optomotor reaction is no more reliable as a means of studying color vision than for tests of visual acuity.

To sum up Birukow's work: He has not demonstrated that the frog necessarily has any reactivity to hue. If his animals *were* responding to hue by such a puré reflex as the optomotor reaction, we can tell no more about whether they have hue *sensations,* by means of Birukow's procedure, than we could with a conditioned-reflex technique. If we even assume that Birukow's conclusions are justified (correcting the one regarding blue) then we must believe that the frog has a 'red' sensation, but no hue sensations from medium and short wavelengths—his neutral point is really a neutral region, which nearly fills his spectrum. But if the animal does also see blue as Birukow claims, then the frog stands revealed as the only known vertebrate whose color-vision system is dichromatic and has a neutral region instead of a neutral point. Until much better evidence than Birukow's is produced, we had best conclude tentatively that the Amphibia have no color vision whatever.

Reptiles—Aside from the age-old supposition that the chameleons can change color to suit any and all backgrounds, and do so because they *see* the colors of the backgrounds, the writer has been able to unearth only one statement about reptilian colorvision from the dark ages of comparative psychology. It was made regarding the common European turtle (*Emys orbicularis*) by an old-time French naturalist. He found that when this carnivorous species is offered a rose leaf, it will ignore it and try to seize the proffering finger; but when offered a rose petal the turtle grasps it at once "because it is the color of a piece of raw meat." This sort of experiment is interesting, but no more than that; and a large portion of its interest lies in the belief inherent in the investigator, and so widespread among laymen, that if any animal can distinguish any hues it should at least be able to recognize those of foliage and blood—the two most important colors for herbivores and carnivores. It seems almost illogical that the hues *yellow* and *blue* should be so favored by psychologists as the 'most primitive' colors in hypothetical phylogenetic schemes of human color vision!

Not until recently was any real investigation of reptilian color vision made, apart from the inevitable pupilloscopic studies and food-visibility experiments of Hess, which showed a shortening of the short-wave end of the spectrum, as in diurnal birds. In 1933, Wojtusiak published his work on a turtle, *Clemmys caspica,* in which a training technique was used, with colored papers and colored lights as stimuli. As with the fishes, intensity-discrimination appeared to be remarkably poor—the turtles

could be trained to distinguish grays only if their shades were very different; but they distinguished each of several colored papers from any of seventeen grays.

Twelve spectral lights were discriminated qualitatively, and the indications were that with longer training a great many more hue differences might have been shown to occur for the species. The trained human observer can distinguish about 160. The spectral limits for the turtle were at least as low as λ401mμ and as high as λ760mμ—much the same as for man and most other vertebrates. Hues were most easily told apart when in the neighborhood of orange-red (λ634mμ), with weaker maxima of discriminability at the blue-green (λ504mμ) and violet, and a minimum in the blue.

The most important hues for the turtle appeared to be orange, green, and violet. Yellow and yellow-green, when not accurately discriminated, were apparently most often seen as orange; but red was separated from the general orange category and seemed to be more akin to violet for the animal, which thus has a closed color circle. These peculiarities were attributed, probably quite properly, to the restrictive filtering action of the meager assortment of oil-droplet colors possessed by the turtle (see Chapter 8, section D). In contrast to the fishes, and in keeping with the predominantly red and orange oil-droplets, the turtle showed an elevated capacity for hue-discrimination in the long-wave region, where also the position of the photopic brightness maximum was shifted from its human (yellow-green) value well into the orange, toward the red. This incidentally is not in keeping with the properties of the turtle's 'zapfensubstanz' (maximum absorption at λ560mμ) as given by Studnitz. The oil-droplets also account for the observed low ability to discriminate hues in the green and especially the blue region, but the apparent slight rise found in the violet region seems paradoxical.

Wagner, a year before Wojtusiak, and working in the same laboratory, published the only study to date on lizards, apart from the peculiar results of Schlieper on *Lacerta vivipara* mentioned above. His technique was simple but effective. He found that *Lacerta agilis* was violently disgusted by the taste of salt. Offering meal-worms pinned in front of discs of colored paper on long handles, he obtained rapid training positive to normal worms presented with one stimulus and negative to brine-soaked ones offered with an alternative stimulus. When each discrimination was finally established, as evidenced by twenty successive correct choices,

Wagner gave the lizard ten additional control trials with both mealworms palatable, thus eliminating any discrimination on the basis of taste, smell, or differential behavior on the part of the salted and unsalted worms themselves.

The most surprising discovery was that it was impossible to train the lizards negative to green. Their preference for this, the most common color in their natural environment, was so strong that when four colored discs bearing palatable food were offered simultaneously, the numbers of times they were approached were: green, 95; yellow, 79; red, 67; blue, 59. When four very different Hering gray papers (numbers 2, 7, 11, 15) were similarly presented, the animals showed no preference for any.

When for twenty successive trials gray, white, or black was offered along with colors on a handle holding four discs, approaches to the respective stimuli were as follows in three such series of trials:

I. Gray, 14; green, 5; red, 1; blue, 0.
II. White 11; green, 5; blue, 2; black, 2.
III. Yellow, 9; red, 5; blue, 4; black, 2.

Thus, gray was preferred to colors—even to green—and white was preferred as if having a value of light gray. Black seemed to have the value of a color, next to blue (which would presumably be seen very darkly, through the yellow oil-droplets present).

Stimuli were thus valued by *Lacerta agilis* in two groups: (*a*) white, grays of all medium shades, and green; (*b*) yellow, red, blue, and black. Group '*a*' was strongly preferred to group '*b*'.

With pairs of stimuli, Wagner obtained discriminations of red, orange, yellow, yellow-green, ice-blue, deep blue, and violet from each other and from any of seventeen grays. In keeping with the presence of only yellow oil-droplets (though Wagner, apparently misled by the situation in his colleague Wojtusiak's turtles, speaks of red ones also), hue-discrimination seemed to be maximal in the red and blue, minimal in the green. These determinations were crude and of course only tentative, awaiting further work by some investigator using a greater variety of stimuli, preferably in the form of spectral lights.

There have been no reports bearing upon color vision in crocodilians, except negative pupilloscopic ones. We know only that the spectral limits of crocodilians correspond with those of mammals; and, from Laurens' work, that the alligator has a Purkinje shift from a scotopic maximum of $\lambda 514 m\mu$ to a photopic one at $\lambda 544 m\mu$.

A majority of snakes are pure-cone, but the strange history which their eyes seem to have had (see Chapter 16, section D) makes it anything but presumptive that they have retained the color vision of their lizard ancestors. If they have color vision, it is *de novo;* but it is unlikely that they do, since their cones are plump (Fig. 26a, p. 63) and their vision, in consequence, is crude and unsharp as compared with other diurnal vertebrates. Experimental evidence is wanting, though Kahmann several years ago mentioned that his training of 'an exceptionally trainable snake species' to red and blue had succeeded quite well. He has apparently published no full account of this work.

Of all the unstudied reptiles, it is the geckoes and *Sphenodon* which offer the greatest interest. There is a large 'hole' in the Duplicity Theory, which can be plugged only when we know whether such forms have retained the color-vision machinery of their diurnal ancestors despite their transmutation of cones into functional rods.

Birds—No one has ever scientifically questioned that the diurnal birds have color vision. Since 1863, when Krause first interpreted the multiplex oil-droplet mosaic of birds as a mechanism for hue discrimination (see pp. 192-3), no doubt of a hue-perceptive capacity on the part of the birds has ever had a chance to grow.

Though color vision was assumed for decades before it was ever proven by experimental work, that work has fully justified the assumption. During the last quarter-century the researches on avian color vision have not had to be wasted in controversy as to whether birds see colors or not, but have been devoted directly to such matters as the determination of the spectral limits, the relative brightnesses of colors for the bird, and the latter's capacity for hue-discrimination in different parts of the spectrum.

For years it was generally believed that the birds are blind to violet and blue, the short-wave end of their spectrum greatly shortened. The work of Hess up to 1912 seemingly established this beyond doubt. Sprinkling rice grains in a spectrum projected upon a white floor, he found that fowls would eat the rice from the red end to the junction of the green and blue, but would peck no grains in the blue or violet lights —allegedly, because they could not see them. The absorption of short-wave light in the red and yellow cone oil-droplets was held accountable, despite the fact that the many colorless cones (and the rods) should have been able to record blue rice—though perhaps hazily, and not *as* blue.

Along with this blue-blindness, a sensitivity to red greater than that of man seemed also to be demonstrated by this early work.

Between 1916 and 1926, the experiments of Hahn, Honigmann, and Blässer painted a different picture. By staining rice grains with different dyes or by illuminating them with colored lights, gluing down the grains to which it was desired to train the birds negative, they showed that the domestic hen does see blue and violet, though weakly. She does have a partial, relative blue-blindness, which increases during growth, presumably because of deepening oil-droplet pigmentations. More important however is her 'blue-shyness', which must be overcome by patient training before she is convinced that blue objects can be good to eat—the best explanation of Hess's results is simply that for a hen, there are no *blue* foods in nature!

In the meantime, some very careful work had been done in this country by Watson and Lashley in 1915 and 1916, but because of the war it went unnoticed abroad for years. They used superlative apparatus affording brilliant beams of pure spectral lights. With a training technique, Watson was able to fix the chick's spectral limits as lying between λ700mμ and λ715mμ at one end and between λ395mμ and λ405mμ at the other. His preliminary experiments upon thresholds for colors indicated that these were about the same as in man, except for the far red to which the chick was somewhat more sensitive. Similar work with the homing pigeon revealed spectral limits of λ420mμ and λ712mμ, indicating that Hess had also been in error in claiming the pigeon to be blind to blue and violet.

Lashley carried on from here, using essentially the same apparatus and procedure. He was able to train his game bantam cocks positive to red (λ650mμ), yellow (λ588mμ and λ565mμ), green (λ520mμ) and blue-green (λ500mμ), and to discriminate each of these from other colored and white lights of any brightness. By changing the wavelength of the negative stimulus, making it closer and closer to that of the positive one until discrimination failed, and repeating this procedure in various parts of the spectrum, he was able to plot a curve of hue-discrimination which proved to have the same number of maxima, in about the same locations, as the corresponding graph for man. The hen's color-vision system is certainly trichromatic, probably essentially identical with our own—though it was independently evolved (consult Fig. 156, p. 519); and the filtering action of the oil-droplets is of course a modifying factor.

Simultaneous color-contrast has been shown to exist for the hen, just

as for ourselves. Révész, in 1921, trained birds to peck rice from pieces of green paper on large gray backgrounds. He then offered them rice on both green-on-gray and gray-on-red combinations. The birds took food from both, showing the 'induction' of greenishness, in the gray, by the surround of complementary red. When offered gray-on-gray, or gray on colors other than red, they were negative. By a similar procedure, blue-yellow contrast phenomena were also elicited.

Few species other than the convenient domestic fowl have been studied to any great extent. Hamilton and Coleman investigated the hue-discrimination curve of the pigeon in 1933. They used a procedure quite different from Lashley's, altering the wavelength of the positive stimulus, by 10mμ steps, toward that of the negative stimulus. The wavelengths near which small differences in hue were best appreciated proved to be 580mμ and 500mμ—values not far from those for man (580mμ and 490mμ). The indications were that in the pigeon the 'green-ness' process (p. 94) does not commence until λ620mμ is reached, instead of at 650mμ as in man; and at λ530mμ the violet-ness process takes complete charge. The pigeon also seemed less sensitive to changes in wavelength than man, though, unlike the fish, it pays much more careful attention to hues than to brightnesses. Where man distinguishes 160 spectral segments, the pigeon can discriminate only 20 between λ700mμ and λ460mμ; but of course the bird's real capacity in this regard is concealed, in any training technique, by its low intelligence. When a human observer is put under instrumental handicaps similar to those of Hamilton and Coleman's pigeons, he may be able to distinguish no more than 20 or 30 hues, as Edridge-Green found. The pigeon was actually able to make discriminations where its human overlords could not; and probably, through the instrumentality of the oil-droplet mosaic, it really has many more hue-experiences than we can possibly help it to demonstrate to us (see p. 502).

The activities of birds are guided almost entirely by vision, but they are the stereotyped actions of an essentially stupid group of creatures. The most intelligent of all birds are probably the parrots and their near allies. The color vision of one of these, the budgerigar or Australian zebra grass-parakeet (*Melopsittacus undulatus*), was investigated by Bailey and Riley in 1931, and independently by Plath in 1935. Bailey and Riley were primarily interested in the budgerigar's ability to form and break psychological associations with colors. Their study of its color vision as such, while technically much more elaborate than Plath's, was beclouded by misconceptions of the nature of hue and saturation. Plath's

work, though based upon colored papers rather than filtered lights (which the Canadians used), yielded rather more useful information.

The budgerigar shows neither the blue-blindness nor the extra sensitivity to red exhibited by the domestic fowl and other birds. Supposedly, this is due to the fact that this bird lacks the deep red oil-droplets present in both hen and pigeon. According to Plath, the parakeet has only orange, yellow, and pallid greenish droplets. The species discriminates blues and violets from grays about as readily as other colors. Grays are distinguished from one another with difficulty (and are perhaps never seen photopically, by any bird, untinged by oil-droplet colors). The curve of hue-discrimination has two maxima, somewhere in the yellow-green and in the short-wave regions—they could not be precisely located with Plath's colored-paper technique. Violet was as often confused with red as with blue, indicating a closed color circle.

Though many investigators have demonstrated a Purkinje phenomenon in diurnal birds by means of pupilloscopic, electroretinographic, and training techniques, not much has been done by way of a comparison of the photopic vision of a single species with its own scotopic vision. Rather, the photopic vision of diurnal birds has been contrasted with the photopic vision of nocturnal birds, and a little has been done with the scotopic vision of the latter.

Piper, in 1905, was the first to make such comparisons. He recorded the retinal action currents under monochromatic lights, and found that the eyes of diurnal birds, such as the hen and buzzard, all gave maximal responses to $\lambda 600 m\mu$, both when light-adapted and dark-adapted. Owls, both scotopically and photopically, proved most sensitive to $\lambda 535 m\mu$. A Purkinje phenomenon for either type of bird was thus denied, though one might speak here of an 'interspecific Purkinje phenomenon', bearing out the Duplicity Theory just as well; for the diurnal birds have few rods and the owls, few cones.

But no bird is known to have an absolutely pure-cone or pure-rod retina, though some are suspected of having no rods and the most nocturnal of all birds (*Apteryx? Steatornis?*) may, when studied histologically, prove to have no cones. All duplex birds *should* show a Purkinje phenomenon, and Piper's results have consequently been questioned many times. In 1907, Abelsdorff first applied to birds the then recent discovery of M. Sachs: that the responses of the pupil to lights indicate directly the relative brightnesses of the lights to the animal. He found the pigeon's pupil to be less responsive to green and blue than the human

pupil. The pupils of four species of owls, on the other hand, contracted more to blue than that of a man standing alongside of them. The procedure was to alternate the same two lights, respectively red and blue, on the different pupils under the same adaptation conditions, watching to see under which light the pupil closed the farther. Having available by chance an intelligent, totally-color-blind man, Abelsdorff dimmed the blue light until this subject's pupil remained unaltered during the alternation of red and blue. Though these two lights were now equal in brightness to the achromatic man, the pupil of an *Athene noctua* still contracted farther under the blue than under the red. Similar behavior on the part of the cat's pupil (in contrast to that of the dog, which responds like man's) convinced Abelsdorff that the greater sensitivity to blue in nocturnal birds and mammals is due to the greater concentration of rods in their retinæ—which also, of course, accounts for any diminished sensitivity to red light (such as occurs in rodents), since the rods are not stimulated by light which rhodopsin does not absorb. The lessened sensitivity of the pigeon to short-wave light was naturally explained by Abelsdorff on the basis of oil-droplet absorption.

Laurens in 1923, and Erhard a year later, between them confirmed Abelsdorff and accounted for Piper's peculiar findings. Laurens found that the pigeon does indeed have a Purkinje phenomenon, but that it takes all of 45 minutes for any discernible effects of dark-adaptation to manifest themselves. Piper had not waited long enough to get actual dark-adaptation, and consequently missed the Purkinje phenomenon; nor had he, like Laurens, used light beams of equal energy content, and he therefore obtained fallacious maxima. With equalized lights, Laurens found that the pupil of the light-adapted pigeon responded between $\lambda 704 m\mu$ and $\lambda 424 m\mu$, maximally at $\lambda 564 m\mu$. Scotopically, the spectrum was shortened at the red end to $\lambda 664.5 m\mu$ and the maximum was shifted to $\lambda 524.5 m\mu$. All wavelengths longer than $524.5 m\mu$ were lessened in effectiveness by dark-adaptation, while the shorter wavelengths had increased pupillomotor efficacy. Comparing the pigeon with man and the alligator, Laurens found that in the pigeon the maximal contraction and dilatation of the pupil were carried out much faster than in man (thanks to the striated iris musculature?), while the alligator's contraction-time was intermediate, its dilatation-time (because of cold-bloodedness, *despite* striated muscles?) slower than that of either man or pigeon.

Erhard, also studying pupillary changes, found that short-wave lights are brightest to owls, less bright to hawks, and least bright to fowls. This

is in perfect keeping with the relative numbers of deeply colored oil-droplets in the three types (see p. 197). Long-wave light had little stimulating value for owls. Ten years later, however, Vanderplank made the surprising announcement that the tawny owl, *Strix aluco,* has a band of visibility in the (human) infra-red, and thus sees its prey, in what for man would be pitch darkness, by means of the prey animal's own body heat. Vanderplank found that a strong beam of $\lambda 900 m\mu$ closed the owl's pupil and seemed to dazzle and frighten the bird, though it had no effect on the human eye. The owl could not find dead, cold prey or chunks of meat in a darkroom—unless they were illuminated by an infra-red spotlight.

Hecht and Pirenne have lately published contradictory findings, though to be sure not on a close relative of Vanderplank's species of owl. Working with *Asio wilsonianus,* the Americans found the curve of pupillomotor effectiveness to be identical with the human scotopic brightness curve (Fig. 35, p. 102), indicating that the photochemical system of the owl's rod is the same as that of our own, and contains nothing in addition to rhodopsin which could give it responsiveness to 'black' light. Vanderplank might have been more perfectly refuted if Hecht and Pirenne had chosen to work on *Strix varia* instead of *Asio*; but recently Matthews and Matthews, studying *S. aluco,* have claimed that the eye makes no response to black-body radiations from 40°C to 400°C, and that the transmission of long infra-red wavelengths through the ocular media is nil.

The spectral sensitivities of such birds, whose vision is certainly entirely achromatic, are of little general interest. But considerable speculation has been offered as to how the world of hues appears to diurnal birds. Naturally, it depends upon the kind of bird—particularly, upon interspecific differences in the oil-droplet mosaic. Where red droplets are numerous, as in song-birds and fowls (and particularly in kingfishers), blues and violets must be seen weakly and unsaturated. Hawks and woodpeckers have few red droplets, parrots perhaps fewer still, or even none in some species. The primary function of the droplets is not to *produce* hue-discrimination (see p. 193); but they do necessarily influence the appearance of colored objects profoundly. Tiny, uncontrollable eye movements appose first one color of droplet, then another, then a colorless cone or a rod, to a given point in the optical retinal image. Each point in space is thus continuously 'scanned' by a succession of filters; and while at any one instant these abolish as many contrasts as they enhance, in the next

instant the pattern changes kaleidoscopically and the net result is enhancement of every contrast sooner or later—and all within a tiny fraction of a second—making for a net improvement in visibilities in general.

The oil-droplets cannot, however, increase brightnesses. Though the red and orange ones may be held accountable for the partial blue-blindness of so many birds, they cannot possibly be what makes the same birds extra-sensitive to red light. Any such peculiarity is due to the photochemical properties of the cones and to their high concentration in the retina. We, too, would probably see reds more vividly in the retinal periphery, if the latter were pure-cone like the fovea. The rods being blind to red light, their interposition in large numbers between the cones is analogous to sprinkling a piece of red paper with gray dots: at a little distance the paper will appear homogeneous but unsaturated, its red chroma weak. Rods lying between the cones of any duplex retina naturally unsaturate all colors by intermingling a grayness-sensation with the colored one from the cones; but in the case of red, they introduce darkness, for they do not 'see' red even as grayness.

Hess was fond of saying that the bird sees the world as we would see it through a pair of orange spectacles. Such a description perhaps covers the dimming of short-wave stimuli, but scarcely the brightening, for the bird, of long-wave ones. Moreover, though the blend of the bird's red and yellow oil-droplets may theoretically be orange, the bird does not have the effect of an orange droplet in each and every cone. If our bird's eye view of things were taken through spectacles composed checkerboard fashion of minute red, yellow, and colorless areas, each just large enough to subtend one cone back in the retina, analogous to the screen of a Finlay or Dufay color-photo, we should *then* be able to gather some idea of how things look to birds. Such a screen would have no such action as that of a homogeneous orange filter.

The possibilities as to manipulation of the ratios of colors in the oil-droplet mosaic are infinite; and we may be sure that some of the extreme ratios we can tally, as in hawks and parrots and kingfishers, and in the red and yellow fields of the pigeon's retina, represent adaptations to aspects of the various birds' ways of life, some of which are still quite unsuspected. Some suggestions have already been given (pp. 195-8). A promising viewpoint is that of Worth and Porsch, who, independently of each other, have pointed out that red and 'fire' colors are extremely common among the flowers which are visited by such birds as honey-birds, humming-birds, etc., and which are dependent upon such birds for their

pollination. Less common, but still very numerous among bird-flowers, are blue-flowered species. Porsch relates the abundance of red-flowered bird plants to the birds' high sensitivity to red (which has been experimentally demonstrated for humming-birds), suggesting that the red of the flower is an identification mark which the bird can pick out from a great distance, and which remains maximally visible against the foliage even in the auroral and crepuscular hours. He raises the question whether flower-visiting birds may not have man-like or superhuman sensitivity to blue light as well as to red—assuming that the plants have actually adapted their flower colors to fit the visual spectra of the birds upon which they depend. Obviously, in the evaluation of avian oil-droplet color mosaics and patterns of spectral responsivity, in ecological terms, the surface has scarcely yet been scratched.

Mammals—Within the mammals, color vision is by no means widespread, as it is in fishes, reptiles, and birds. To a large degree this is simply an expression of the fact that strong diurnality is uncommon in mammals. But, not even all diurnal mammals have color vision. This would be particularly hard to understand if the few diurnal mammals were all primitive and stood closer than other mammals to the reptilian stem. The birds, for instance, clearly owe their chromatic vision to direct, unbroken inheritance from reptiles—possibly avian color vision traces back through the reptiles to the Stegocephali, or even back through them to the fishes (Fig. 156, p. 519).

The indications are, however, that on the road of *mammalian* evolution there was a considerable stretch of achromatic nocturnality between the color-seeing reptiles and the first color-seeing placental mammals. Strong or strict diurnality, backed up by a cone-rich or pure-cone retina, is not a primitive habit of mammals. Nor can it be said that diurnality has arisen in the mammals only as one of the specializations and points-of-superiority of the 'highest' forms. Though the larger ungulates and carnivores tend toward diurnality, in that they have become arhythmic from nocturnal beginnings, it is only the squirrel and monkey tribes which present fully diurnal members. The squirrels are rodents, which rank fairly low—but even they must be given rank above *us*, in point of 'specialization' and 'modernity'. We, as primates, adjoin the very lowest of all the orders of placental mammals, the Insectivora. All of our domestic animals roost far higher in the taxonomic tree than we ourselves—a point which is overlooked by some writers on comparative ophthalmology, who

would as soon as not derive some structure in the human eye from something or other in the eye of a horse.

Diurnality, with its expectation of color vision, is thus a habit which, so far as the mammals are concerned, has cropped out only in forms a little removed from the bottom of the heap—and a great way from the ungulates and carnivores which sit on top. In a survey of the mammals, we can perceive no majestic progress in the evolution of color vision from an imperfect system in primitive groups to a complex one in the highly specialized orders. On the contrary, we find a fully-developed color system only near the roots of the class, in the primates; and in the higher subdivisions there are only the most rudimentary of color-senses, if any. So, to avoid anticlimax, we can best review the subject of color vision in mammals in reverse order, starting with the higher groups and progressing to the lower ones.

The ungulates afford a classical supposition: that male cattle are infuriated by red objects. In 1923 Kittredge began some experiments with a calf which yielded only negative results as far as they went, but were unfortunately never concluded. In the same year Stratton summed up some simple experiments as indicating that cattle pay as much attention to green as to red, more yet to white, and are most aroused by any fluttering object, whatever its color may be—especially when the object is unfamiliar. Red has no special emotional value, hence cannot be assumed to arouse a distinct sensation quality. A whole herd of European stud bulls were once provided with red veils, which entirely failed to disturb their equanimity.

Oddly enough, the horse has never been the subject of any extended study of color vision. Large animals are not in favor with psychologists as experimental material, for obvious reasons; but even so, the docility and intelligence of the horse qualify him admirably for exploitation. As indications of color vision, however, we have only such items as the old report that a French army horse, in North Africa, was able to distinguish his master in a red uniform from other men in blue ones, at a distance of 600 meters—a hundred meters farther away than he could make the distinction without benefit of the color-difference in uniforms. But, there is nothing here to show that the discrimination was on the basis of hue rather than of brightness.

Among the carnivores, the dog, cat, raccoon, and two mustelids—the European stone- or beech-marten and the polecat—have been studied. Color vision was affirmed for the dog by Gates in 1895, Himstedt and

Nagel in 1902 and 1907, and Colvin and Burford in 1909. Lubbock, in 1888, Nicolai and Orbelli in 1907 and 1908, denied it. None of these investigators adequately excluded discrimination on a basis of brightness. Nor was brightness controlled properly by Kalischer, working in this period, though he did use colored lights. One of his dogs could distinguish a red light readily from a blue one, less readily from other colors. One reaction which Kalischer did obtain, and which speaks strongly for a qualitative perception of hue, was a sharp withdrawal of the dog from a blue light.

The first impeccable experiments were those of Samoiloff and Pheophilaktova in 1907. They found that dogs confused colored papers with gray ones of various shades; but they were not confused so consistently as to make it certain that discrimination was wholly lacking. The best results were obtained with green—the dog could not distinguish it readily from dark grays, but showed some improvement with practice. When the shape of the green paper was changed, the animal more often chose the negative, gray paper which was of the old familiar shape. The investigators concluded that form is far more important to the dog than color, if indeed the animal experiences color at all.

Smith, in 1913, worked with seven dogs which she also trained to colored papers. For any given color, some group of grays in her long Nendel gray series gave the dog great difficulty in discrimination; but Smith was unable to find any gray which a given dog would always confuse with a particular color. The animals could tell grays from each other better than from colors; but Smith concluded that at least certain individual dogs have an unstable color sense, so very rudimentary as to be completely unimportant to the animal. For the dog, it is form and (to a less extent) brightness which are important qualities of visual stimuli. Whatever weakly chromatic sensations his cones may afford are further unsaturated, greatly diluted, with 'grayness' stemming from his superabundant rods. To any such semi-nocturnal, rod-rich animal, the richest of spectral lights could at best appear only as delicate pastel tints of uncertain identity.

For the domestic cat there is even less evidence of any color vision whatever. Colvin and Burford, while they thought there was positive evidence from their work in the case of the dog, claimed none for the cat. De Voss and Ganson in 1915 reported a study of nine cats, in which training to colored papers of controlled albedo and texture was involved. For every cat and every color, a particular gray paper was found which was completely confusing. When the training color was placed among

the 89 samples of the entire Bradley color set, the cat would pick out not only it, but several others as well. Pavlov, it may be noted, was never able to establish in the cat a conditioning of reflexes to hue, and was partially successful with a dog only after 3000 trials.

Gregg *et al,* in 1929, attempted to train a cat positive and negative to different combinations of filtered lights arranged like Ardois signals; but when gray stimuli of equivalent brightnesses (for the human) were substituted for the various colors, the animal responded just as though the colors were still there. The investigators concluded that the cat is totally color-blind, or that at any rate colors have absolutely no significance for her.

Only Kalischer has claimed that cats easily discriminate hues. His 1929 report on the subject is very sketchy. He claims to have varied the intensities of his colored lights sufficiently to exclude a brightness-discrimination, but he does not give enough details to enable one to be at all sure—especially when it is borne in mind that cats certainly see short-wave lights much brighter (as indicated by their pupil responses) and probably see long-wave ones much dimmer (because of the great predominance of red-blind rods) than we do. It is particularly reprehensible, in the case of nocturnal mammals, to assume that the relative brightnesses of colors are the same as they are for humans. It can very reasonably be assumed, always, that they are *not.* Another method of Kalischer's—'training' the cat positive to undyed, negative to dyed, meat—is open to the serious criticism that he made no attempt to rule out olfaction. So finicky a feeder as the cat would assuredly need no training to avoid food which did not smell quite right to her. We can be quite sure that the cat has no hue-discriminatory capacity at all; and we might paraphrase the old saw to read: "Day and night, all cats see gray."

None of the various researches on the raccoon is very complete. Cole's first work, in 1907, was not properly controlled. With Long, in 1909, he succeeded in getting raccoons to select a colored paper, or the gray, from a series of five colors and one gray all of which had the same albedo (in flicker photometry) for the human eye. These investigators also tested the animal's ability to discriminate brightnesses, and found it excellent. But their conclusion—that the animal has some color vision—was unjustified inasmuch as they made no effort to match a color with a gray in brightness for the raccoon. Davis, in 1907, was not even able to train raccoons to colored stimuli which were of equal brightnesses for man. Gregg *et al,* with the same procedure which had yielded only negative

results on the dog and cat, obtained only negative results also with the raccoon. This species is thus in the same boat with the dog: if it has any color sensations, they are so vague and unsaturated that some individuals are not even conscious of them at all; and to other individuals, they cannot be made to have meaning.

Despite the alleged interest of the mink in red objects, the mustelids which have been studied at all carefully have shown no evidence of having color vision. Müller, in 1930, dyed some hen's eggs red, green, blue, gray, and white. His captive marten (*Martes foina,* a close relative of our *Martes americana*) was allowed to come for them and take them, one by one, to its cache in a corner of the cage. The animal took the eggs in various sequences in successive tests, evincing no indication that any one egg seemed brighter than another or that any color was especially attractive or repellant. Müller's extensive studies of the psycho-physiology of this species led him to rank olfaction above hearing in importance for the animal, with vision a poor third on the sensory list.

Müller did more work with the polecat, *Putorius putorius,* a type of mustelid for which there is no exact American counterpart, but which is the wild ancestor of the domestic ferret seen here occasionally in the capacity of professional rat-catcher. Müller rated the sensory modalities of the polecat all lower than those of the stone-marten, but in the same order of value. The polecat could be trained to discriminate brightnesses, but not colors. It was taught to distinguish between red and blue papers, but when these were placed among other colored and gray papers the animal was lost. The species is either totally color-blind or perhaps, like the dog and raccoon, excessively color-weak. All in all, the evidence for color vision in carnivores is practically nil.

Turning to the rodents, we find ourselves in a most controversial subject. On some of the selfsame species, equally strong claims both for and against color vision have been advanced. While the squirrels are set off sharply from other rodents by their diurnal habits and cone-rich or pure-cone retinæ, strangely enough the evidence for color vision in them is no better and no worse than that relating to some of the most strongly nocturnal rodents, whose possession of any cones at all is questioned by some retinologists.

In all, three kinds of squirrels, six other rodents, and one lagomorph have had experimental attention. Most of the studies have been made upon the common laboratory species. Watson and Watson, in 1913, studied the rat with a spectral light technique. They trained rats positive

to yellow (λ595mμ) and negative to darkness. When a blue (λ478mμ) of low intensity was substituted as the negative stimulus, the rats continued to go to the yellow. But when the intensity of the blue light was increased to a certain point, the rats broke down and made chance scores. One rat was trained positive to red versus green. Removal of the green stimulus confused the animal, which made chance choices; but removal of the 'positive', red, stimulus had no effect. Obviously, the red stimulus was no stimulus at all—the rat was blind to it. This shortening of the red end of the spectrum is quite in keeping with the fact that the rat, like all other known rodents, exhibits no Purkinje phenomenon either electroretinographically or pupilloscopically. This, despite the unquestionable presence of some cones, in a proportion of perhaps one to every hundred or more rods.

Munn, in 1932, used colored papers with the rat and obtained only negative results. Several years later, with Collins, he reinvestigated the rat's perception of red light. The red stimulus was paired with a 'negative' white light and with darkness in alternate sets of trials, the object being to make impossible any step-wise response always to the brighter stimulus, and to avoid giving the rat any constant stimulus to which he could become negative. The animal was thus forced to react positively to redness alone if it could; but it proved unable to do so with any regularity. The authors concluded that for the rat the brightness-relation of the stimuli was of most importance, their absolute brightnesses secondary, and that color discrimination—if any—was indeed weak. These results verified those of Muenzinger and Reynolds, whose technique had been similar except for the use of red, white, and black papers instead of red and white lights and darkness. The rat had shown an ability to discriminate red from gray, but with great difficulty when the gray was close to black. This again would be expected if the rat is blind to long-wave light.

The work of Coleman and Hamilton has been considered, by psychologists, a model investigation. In 1933, they trained rats positive to black versus red. When gray was substituted for the black, and when the red was exchanged for a darker shade, the animals reversed their preference. Reversal of the brightness relationship in other pairs of color stimuli also inverted the responses of the rat. With some pairs, only chance scores were ever made, showing that the two stimuli were not only matched in brightness but had no difference for the animal as to hue. When new rats were introduced to these 'confusion pairs' of colored papers, they could never learn to go to one paper and avoid the other.

Walton, however, has insisted that the rat has color vision. In 1933, he trained rats to large patches of filtered colors, the two members of each pair of stimuli being matched in brightness for the human eye at first. The animals readily learned to discriminate red from green, blue, and yellow, and to tell blue from yellow. Their discriminations of green from blue, and of yellow from green, were not high but were better than chance. When one member of a pair was increased in brightness, the animals continued to make the proper choice. Walton concluded that the rat has hue sensations; but the Watsons had shown that the rat's brightness curve is enormously different from man's, and Walton made insufficient efforts to find a point of matched brightness for any pair of stimuli. With Bornemeier in 1938, Walton used red and blue stimuli and satisfied himself that the rat discriminated them solely on a basis of hue. His animals also discriminated red versus darkness; but, far from the red's being all but invisible to them, they behaved as if they were 'rather sensitive' to it when in a condition of semi-dark-adaptation.

Walton's methods are not sufficiently different from those of other students to make it at all easy to see why he gets such unique results. Majority opinion seems to be that until his work has been abundantly confirmed, it must be held to conceal some unknown errors of procedure.

For the house mouse, as for the laboratory rat, the great weight of evidence is negative; yet here again a single investigator has claimed positive results with what seems to be adequate technique. In his classical study of the dancing mouse in 1907, Yerkes reported that the mouse could discriminate between filtered green and blue lights only when they differed greatly in intensity. Green versus red, and blue versus red discriminations were easily learned; but when any colored light was replaced by colorless, the mouse went to the less bright of the two stimuli. Red light was only responded to as the brighter of two lights when it was of very high intensity. As in the case of the rat, the spectrum of the mouse appears to be shortened at the long-wave end.

The preference for dim *lights* is in interesting contrast to the mouse's strong preference for white and bright-colored *papers* (as nest-building material), as reported in 1934 by Kolosvàry. This worker's animals preferred blue paper to red however, which would be expected from his other results since the invisibility of the redness of red papers would naturally make such papers appear dark to the mouse.

Hopkins, rejecting the work of Yerkes and the later, also negative, findings of Waugh and Roth, described in 1927 some experiments on

mice with both normal and 'hereditary rodless' (Keeler) retinæ. He found reason to think that some individual mice have a rudimentary color sense. Most of his animals could not discriminate colored papers from grays or colored lights from white ones, but one mouse out of seven could distinguish a red light from a white one—though the same individual confused red papers with gray ones. But we should expect that if red light is of no stimulating value it would naturally be discriminated (as *darkness*) from even a dim white light, whereas a red paper would not be *invisible,* even though its redness was not registered, but would appear gray and would be confused with gray papers. Despite this sort of criticism of his work, Hopkins remains to the mouse what Walton is to the rat: the sole claimant of color vision; and the same remarks apply to both—their techniques are not discernibly superior, if equal to, those of the larger number of other investigators who have found no reason to think that murid rodents see hues as such.

The rabbit has come in for some attention. The Watsons found, as in the case of the rat, that after red-versus-green training, darkness could be substituted for the red light without disturbing the animal in the slightest: red light *is* darkness for the rabbit. The animal was now trained positive to a blue light and then was required to discriminate it from a dim yellow, which was gradually brightened. The animal died before the investigators were able to try a range of intensities sufficiently great to exclude a brightness discrimination. They were only able to say that blue light probably looks brighter to the rabbit than a yellow of the same energy.

At about the same time (1912) Washburn and Abbot were experimenting with six rabbits, using colored papers. The animals learned to distinguish a red from a light gray, but could not tell the red from a dark gray or a black. The results with blue-gray discriminations were not so striking, but did permit a conclusion that only brightness guided the rabbit to a choice.

Again, as with the rat and mouse, there is conflicting evidence. R. H. Brown, in 1936, claimed to have established a Purkinje shift in the rabbit, from $\lambda 560 m\mu$ to $\lambda 530 m\mu$; but his procedure was altogether too crude to support his conclusions. He established a reflex response to colored light by conditioning with light and shock stimuli. His animals were quickly made responsive to only one member of a pair of lights ($\lambda 640 m\mu$ and $\lambda 490 m\mu$), but his variation of the intensity of the negative stimulus was made in only three large steps—scarcely adequate to

spot a point of matched brightnesses. Brown's technique is promising, but in his hands it has yielded no evidence of color vision in the rabbit.

Another piece of work which would bear careful repetition is that of Sgonina, in 1936, on the guinea-pig. This animal's retina is even more certainly a pure-rod one than that of the rabbit; yet Sgonina claims that it is able to discriminate between colored papers whose difference in brightness is less than that which must exist between two gray papers, if the guinea-pig is to discriminate the latter. He found that two grays could be told apart only when one was about one-third brighter than the other. The validity of his conclusion obviously hinges upon the correctness of the assumption that a guinea-pig sees the brightnesses of colored papers as Sgonina himself did—and we have seen, *ad nauseam,* that such an assumption must never be made.

Sälzle, also in 1936, studied two species of wild mice. He found that despite its excellent learning capacity, the European long-tailed field mouse (*Apodemus sylvaticus*) was hopelessly confused when a red light was offered it alongside a yellow or green to which the animal had been trained to go. The red-backed mouse (*Clethrionomys glareolus*) told a different—and unique—story:

Animals trained to filtered red light readily learned to distinguish it from green, blue, and yellow. Animals trained to green quickly learned to discriminate it from red; but when offered green versus yellow their discrimination was poor and, though it improved rapidly, never became perfect. Offered green versus blue, they failed completely. Sälzle then trained two animals to each of the four colors, and offered each of the animals all four colors at once, their positions being changed from trial to trial to avoid position habits. The result was that the animals trained to red or to yellow went mostly to red or to yellow as the case was, but the animals trained to green went about equally to green and blue, and the animals trained to blue went equal numbers of times to blue and to green. Sälzle was sure that the apparent equivalence of the green and blue stimuli was not due to their being matched in brightness for the animal—but his evidence for this was that the green light was much brighter than the blue one for his own eye. We would expect a human green-blue brightness-match to be no match to achromatic rodents; for their scotopic and photopic brightness curves appear to rise from zero in the red to a maximum in the blue-green or blue. A green which matched a blue for them *would* look brighter than the blue to a human.

The two green-trained animals were now investigated further, with one green and three blue stimuli offered simultaneously in varied positions. Assuming that the animal could not discriminate the stimuli, it should have gone 25% of the time to the green stimulus and 75% to the various identical blue ones. One of the mice went to green ten times and to blues 38 times (21%-79%). The other went to green 16 times and to blue 32 (33.3%-66.6%). Sälzle felt confirmed in his judgment that for this animal green and blue are qualitatively identical. He attempted, quite unsuccessfully, to fit this into the framework of either the Hering or the Young-Helmholtz theory of color vision. But the strong probability is that the animal is achromatic and that the particular green and blue were a match for it in brightness—Sälzle is most vague concerning his alterations of intensity, and his text gives no assurance that this factor was controlled.

Lastly, for nocturnal rodents, may be mentioned Sackett's (1913) negative results with the porcupine. The absence of color vision in such rodents, all of which have few cones (or even none), is no surprise. But in the diurnal squirrels, whose retinæ contain no visible amount of rhodopsin and appear to contain only cones (this being certain in the case of the ground-squirrel and prairie-dog), color vision would be expected—indeed, a color vision about as rich as that of our own foveal region, though of course affected in the short-wave realm by the presence of a yellow filter, the lens (see p. 199). In the light of this expectation, the results of experiments on squirrels are most interesting:

Colvin and Burford, in 1909, were able to train a native squirrel positive to a pigmentary red and negative to either another color or a gray, all the stimuli having the same brightness to man. They drew the unwarranted conclusion that the squirrel, like their dogs, discriminated the hues as such. Sälzle also worked on one specimen of the European squirrel (*Sciurus vulgaris*), training it first positive to green, then to red, and offering three negative color-stimuli with each. The animal had no trouble in making all discriminations. Sälzle states that with each pair of lights, one or the other could be made brighter or darker, or the two about the same brightness (for his own eye) without it making any difference to the animal's ability to tell them apart. But no attempt was made to match their brightnesses for the animal, and no details are given as to just how intensity was varied.

In contrast to these imperfect and inconclusive studies we have the extremely careful work of Charlotte Locher which, though offered as a

preliminary report, seems a truly model investigation. She reported, in 1933, on three *Sciurus vulgaris,* which she had trained with red, blue, yellow, and green papers and with the Hering series of 30 grays. The first animal was trained positive to red versus gray, and proved unable to discriminate red from any dark gray. Substitution of another gray for the red produced no disturbance in the sensitive creature, indicating that the squirrel sees red objects as gray. It would go to the darker of two grays, and when offered a blue versus a (darker) gray the animal did not go to the blue at all until after three days of trials.

The second animal also failed to discriminate red from dark grays, and could not distinguish green from light grays. Yellow was discriminated from the very lightest grays about three times out of every five trials, and was readily distinguished from medium and dark grays. Green was completely confused with the three lightest of the grays. This individual, then, saw red and blue as dark gray, green as a light gray, and yellow probably as a very light gray, though the possibility of a qualitative difference of yellow from gray could not be denied.

The third squirrel had no trouble whatever in telling yellow from all grays and white. Unless the yellow paper appeared to him even brighter than white (which is possible, but seems unlikely in view of the performance toward green and blue) this means that the animal saw yellow as a distinct quality. It was also able, after extra practice, to discriminate light green from all grays, though it never learned, in 236 trials, to tell a rich green from the darkest gray. It was also very difficult for this individual to learn to tell blue from grays, though it finally succeeded in maintaining an 80%-correct average on the most troublesome sequence of five adjacent grays. Red was confused completely with all but a few of the lightest grays, as in the other two squirrels.

Of *Sciurus vulgaris,* one can apparently say about the same thing as of the dog: a weak hue-discriminatory capacity may be present—but so very weak that, within the limits of normal individual variation, it may be entirely lacking in a particular individual.

The ground-squirrels are even more certainly pure-cone than the tree squirrels typified by *Sciurus* spp. One of them, the souslik (*Citellus citellus,* the European counterpart of our thirteen-lined spermophile) was studied by Kolosvàry; but only as to color preference. When offered strips of white and red paper as nesting material, the animal at first took twice as many white ones as red, later became used to the red and took about equal numbers of both. When white, blue, and black strips were

given, the souslik preferred the blue strongly, and white and black equally. Given red, white, and blue pieces, it took blue slightly oftener than white, and either about twice as often as red. This order of preference—blue first, then white and black equally, then red—does not quite check with the tree-squirrel's preference always for the darker of two stimuli. The lens of *Citellus* is so strongly yellow that blue paper should appear darkened, as red does to *Sciurus vulgaris* or to nocturnal rodents. Even the *vulgaris* lens, which is probably pallid compared with those of other squirrels, absorbs some light from λ436mμ on—*all* light from λ400mμ onward, according to Merker. But the equal value of white and black for the souslik seems a paradox.

Leaving the rodents, we come at last to the primate order. Here, as with the birds, there has never been any doubt of the occurrence of color vision in all its glory. Among the species in the higher (Anthropoidea) sub-division of the order, the chimpanzee, the Guinea baboon (*Papio papio*), the pig-tailed macaque (*Nemestrinus nemestrinus*), *Pithecus fascicularis,* the rhesus monkey, the sooty mangabey (*Cercocebus torquatus*), squirrel and spider monkeys have all been studied. The work of Kinnaman (1902), Köhler (1918), Bierens de Haan (1925), Kohts (1928), Trendelenburg and Schmidt (1930), Klüver (1933), Brecher (1936), and Grether (1939, 1940, 1941) on these forms has shown that their hue systems are identical with the human one to all intents and purposes. None of this work whatever is negative in implication.

The few investigations to date upon the lower primates, the Lemuroidea or Prosimiæ as opposed to the Anthropoidea or Simiæ, have yielded only negative results. In general, this is to be expected, for most of these lower forms are strongly nocturnal whereas all of the higher primates except the douroucoulis or night monkeys (genus *Aotus=Nyctipithecus*) are diurnal. Some, at least, of the prosimians are pure-rod.

But among these lower primates there are two groups of genera whose habits are opposite to those of all other lemuroids—just as *Aotus* stands out as a rebel among the anthropoids. These are in the sub-families Indrisinæ and Lemurinæ. In the former, the avahis (genus *Lichanotus*) are strictly nocturnal, but *Propithecus* is diurnal and crepuscular and the black indris (*Indri indri*) is diurnal. Among the lemurines there are also several nocturnal genera; but *Hapalemur* is diurnal and so are all of the many species of *Lemur* itself.

One of the true lemurs, *Lemur mongoz,* was investigated in 1930 by Bierens de Haan and Frima, who fully expected the species to exhibit a

full color-vision system like that of other diurnal primates. One of their two specimens proved to be totally color-blind. Trained to colored papers, it was confused by gray ones—by dark grays with red and green, medium grays with blue, and by light grays apposed to yellow stimuli. Only a training-to-brightness was possible; and this was readily switched over from responses to red versus blue to green versus yellow stimuli, and from green versus yellow to dark gray versus green. In both of these cases, a color-seeing animal would have been quite befuddled by the change.

The second individual was trained to blue only. It could then be confused by grays of a particular sequence, but did somewhat better as time went on. This lemur was disturbed when switched from blue versus red to light gray versus red; but since for the other animal blue was matched by *medium* grays, differences in behavior toward blue and light gray are not at all surprising and prove nothing as to color vision.

The authors consider that if an animal makes no more than 30% errors in a color-versus-gray discrimination it cannot be considered totally color-blind. But, even if such a liberal allowance be made in this instance, we cannot credit the lemur with having any more vivid color experiences than the carnivores and the rodents. The situation in the lemurs—in which diurnality is already firmly entrenched but whose color-sense is only in its faintest beginnings—is the best of evidence for thinking that primate color vision has arisen wholly *within* the primate stock.

The situation in *Cebus,* as reported by Grether (1939, and in correspondence with the writer) is especially interesting. Grether's four individuals, of two species (*C. unicolor* and *C. capucinus*), all gave every evidence of being protanopic dichromates, with lowered sensitivity to red and with a neutral point at about $\lambda 515 m\mu$. Watson's (1909) data on one *Cebus* are reconcilable with Grether's findings, though Watson's procedure was not such as to reveal dichromasy in his animal. This one genus, then, *may* have a dichromatic system as its standard equipment.

The diversified Cebidæ and the more homogeneous Hapalidæ (marmosets) comprise the platyrrhine (New-World) division of the Anthropoidea, opposed to the catarrhine series of Old-World forms. The platyrrhines and the catarrhines are usually considered to have had quite independent origins from lemuroid stock. If the lemuroid ancestors of both had color vision, then all primate color vision stems from a single beginning. If however the lemuroid common ancestor of all the monkeys lacked color vision—as seems likely—then color-vision systems have developed separately in the platyrrhines and the catarrhines. Again,

while all catarrhines are diurnal and trichromatic, there remains a possibility that the trichromasy known for some cebids (*e.g.*, the squirrel monkey, *Saimiri sciurea,* and the spider monkey, *Ateleus ater*) has evolved through a dichromatic phase in other cebids (*i.e., Cebus*).

The marmosets are less distinct from lemuroids than are the lowest catarrhines, and may be ancestral to the Cebidæ rather than derivatives thereof—no one can be sure. In any case, nothing is as yet known about their color vision. Among the cebids the nocturnal, assuredly achromatic *Aotus* may be the most primitive,* though this honor is usually accorded to the closely-related diurnal genus *Callicebus,* whose color-vision status is unknown. A case, of sorts, could thus be made out for considering that trichromasy has evolved independently in the catarrhines and platyrrhines, and through achromatic (*Aotus?* marmosets?) and dichromatic (*Cebus*—and *Callicebus?*) stages in at least the platyrrhine series, if not through equivalent (but missing) links on the catarrhine side.

Below the primates there lies but one order of placental mammals, the Insectivora, regarded by taxonomists as ancestral to all other placentalia and as immediately ancestral (even osculant, through such forms as *Tarsius*) to the primates. Some insectivores (the tree-shrews, *Tupaia*) are strongly diurnal; but their vision has yet to be investigated. Only the common European hedgehog, *Erinaceus europæus,* which is nocturnal, has had attention.

Herter and Sgonina reported on this animal in 1933 and 1934. They could not get their hedgehog to go to a yellow paper and avoid a blue one—it insisted on going to the blue, so the investigators allowed that to be the positive stimulus. Subsequent substitutions of other colored and gray papers for the original stimuli revealed that the animal would usually choose the darker of any two stimuli. The results suggested that the hedgehog could see yellow, but no other color, as a quality distinct from gray; but this conclusion hinged upon the outmoded Hessian assumption that equal brightnesses for man are equal brightnesses for animals. This is extremely unlikely in the case of the hedgehog, a nocturnal, apparently pure-rod animal. Miss Locher has offered other criticisms, which Herter and Sgonina have failed to eliminate in their second contribution. The hedgehog may have a color-life comparable with that of Locher's second squirrel, but it probably has no color vision at all.

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*Though the fact that its tapetum is utterly different from that of the lemuroids (p. 233) suggests rather that the nocturnality of *Aotus* is secondary.

Of possible color vision in some of the most nearly diurnal marsupials, the kangaroos and wallabies, we know nothing. For the monotremes and marsupials together, there is only the single entirely negative report of Sälzle on an opossum species, *Didelphis paraguayensis*. But the retention of the cone oil-droplets during so much of mammalian evolution, past the monotreme level and into the marsupials, suggests that these lower subclasses were not always as strongly nocturnal as their surviving representatives (the kangaroos excepted) are today.

Phylogeny of Color Vision—In digesting the above survey, the reader may have been struck by the fact that the groups of vertebrates which possess full-blown color vision are the very ones which have evolved excellent mechanisms of accommodation: the teleosts, the sauropsidans, and the primates. This relationship is not accidental. These are the groups which are more eye-minded than otherwise, and whose retinal visual acuity is high enough to deserve refined optical images and to make hue-differences a useful factor in the perception, identification, and evaluation of visual objects. They are the only groups in which a fovea is ever seen. The bright-light habit depends upon cone-richness, affords high visual acuity, demands good accommodation, and supports good hue-discrimination. It is only natural, then, that these phenomena are found in association.

The color-vision systems of these three vertebrate groups are probably just as independent of each other, in point of origin, as are their methods of accommodation. If they are physiologically identical or nearly so (and they certainly appear to be), it is because, like so many other simpler, discontinuously-distributed and repeatedly-evolved entities (lentiflavin, rhodopsin, melanin etc.) they have developed out of a substrate of chemical and physiological potentialities which is common to all vertebrates. In other words, the systems are homoiologous.

We know nothing about the possible color vision of non-teleost fishes. The lampreys, some species of which have at least 50% cones, may conceivably have it, though it would be hard to say what its value might be to them. The elasmobranchs are all pure-rod excepting *Myliobatis aquila* and *Mustelus* spp., which have few cones. But at least one of the holosteans, *Amia*, is known to have a teleost-like retina and habits; and when eventually investigated this may prove to be the group which really invented teleostean color vision.

The extinct crossroads group of the Stegocephali, which were almost certainly diurnal, may have shared with the teleosts the inheritance of

an original chondrostean color-vision system, and may have passed it on to the reptiles and, through them, to the birds on the one hand and the mammals on the other (Fig. 156). If so, the modern amphibians lack color vision because they have discarded it as something useless in their mode of life. Since no living color-seeing forms bridge the gap

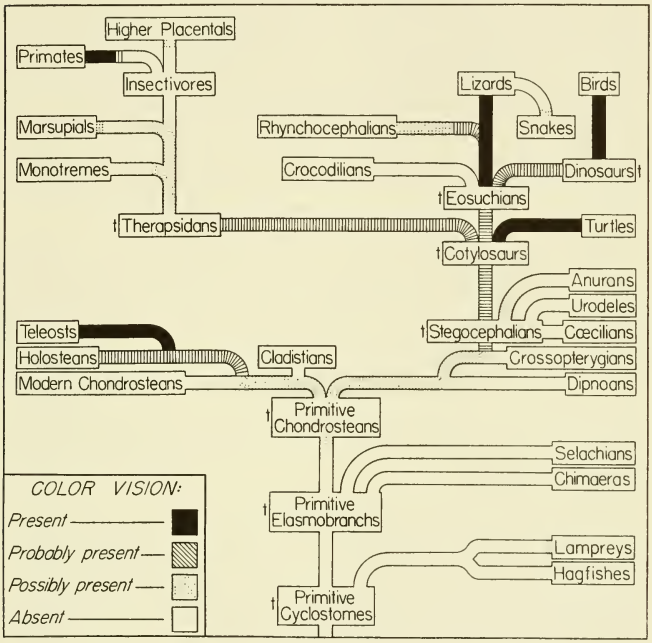

Fig. 156—The probable phylogeny of color vision in vertebrates.

between the turtles and the fishes, we probably have no right to suppose that the sauropsidan and teleostean color-vision mechanisms represent only one single invention of long duration and wide distribution—at least, not until the holosteans are shown to discriminate hues. Unfortunately, no diurnal chondrosteans are left on earth.

Exclusive of the placental mammals, then, color vision has been elaborated perhaps only once (by the chondrosteans, passed on by them to the stegocephalian-reptilian-avian series as well as to the teleosts), perhaps twice (by the holosteans or teleosts and later, independently, by the early reptiles [cotylosaurs], which gave it to the birds and maybe to early diurnal mammals). Then too, color vision may have been developed *de novo* within some reptilian groups. For, just as the transmutation of cones into rods in such forms as *Sphenodon,* the geckoes, and the Xantusiidæ may not necessarily have abolished color vision (gecko rods, Crozier and Wolf have found, respond to flicker like turtle *cones*), so also color vision may have been regenerated or re-invented where cones have secondarily reappeared. *Dryophis et al* will be most interesting in this connection—if color-vision researchers sometime find a way to 'motivate' them— as would also the diurnal geckoes such as *Phelsuma,* whose visual cells were once lizard cones, then gecko rods, and are now probably cones once more.

However few or many times color-vision mechanisms may previously have arisen in vertebrate evolution, the color vision of the higher primates is assuredly a law unto itself, genetically and historically speaking (see Fig. 156). The absence of color vision in the lowest primates, the lorises, galagos, tarsiers and the like, might mean only that these had discarded color vision by discarding cones in order to become nocturnal. The indications are overwhelmingly against such a view. The primates originated as a nocturnal group, from nocturnal, rat-sized insectivore ancestors which may not even have kept any of the cones of their therapsidan forebears.

The placental-mammalian cone looks most suspiciously as though it had arisen by transmutation within the subclass. It is never double, never has an oil-droplet or a paraboloid, never migrates. The placental mammals evolved through the restrictions of the nocturnality of the early insectivores. Like the snakes, which had an even worse time being born from the lizards, they probably produced an entirely new crop of cones, which consequently are quite unlike those of the lower mammals and the Sauropsida. Holding this viewpoint, it becomes easier to understand why it is that although cones are numerous and widespread among arhythmic and diurnal placental mammals, yet color vision is not. To acquire color vision, each group of such mammals would have to start from scratch; and only those have made this start, whose vision means so much to them that color vision is a real desideratum.

Just as diurnality has surely arisen by slow degrees within the primate group, so also has human color vision developed entirely within the primate order. We might expect to see color vision in the true lemurs—as also in the diurnal squirrels—but it is not there. Only entirely above the lemuroids has the final refinement of color vision been added to the prerequisite diurnality, and it is quite possible that this addition has been made independently in the platyrrhines and the catarrhines (*v. s.*).

It seems necessary to believe that human color vision owes nothing whatever to the product of the teleost and the reptile. But 'human' color vision is already present far below man in the anthropoid stock. It is not necessary to suppose, with Bierens de Haan and Frima, that human color vision has evolved wholly within the genus *Homo*. True, it was once believed that the ancients of Greece and Egypt had an incomplete color vision as compared with modern man. The situation is now realized, however, to have been due to a simple paucity of words for colors in the languages of archaic and primitive peoples—the Homeric vocabulary, for instance, contained no word for 'blue'. The Japanese use the word *ao* for both green and blue—but they see a difference between them.

Locus of Color Vision—We know that whenever color vision did arise, however often it may have done so, it involved a differentiation of several coöperative sensation-processes in the central nervous system, as well as a set of differentially photosensitive chemical substances in the visual cell (see Chapter 4). These latter, however, may be universally present in cones, several such substances being needed in order to fill out neatly the responsivity of the visual cell, to embrace as fully as possible the spectrum which the watery dioptric media of the eye will let through. It seems highly significant that the electrophysiological images of hue-stimuli show the same hue-specific character in achromatic animals (*e.g.*, cats, rabbits) that they show in color-seeing forms. The evolution of a color-vision system very likely entails only the affiliation of specific central processes of registration and integration with particular photochemicals already present in the cones.

Where, in the central nervous system, are these hue-sensory processes placed? We can say a little, though not much, on that point. In the lower vertebrates, the optic nerves (in their continuation as the optic tracts, quite unmodified since the decussation is total) sweep directly up to the optic tectum, the roof of the mid-brain. A few fibers do terminate in other minor centers; but the connections of the tectum with the centers

controlling extra-ocular, intra-ocular, and skeletal muscles make the optic tectum very much the chief center for visual reflexes. Whatever visual consciousness a fish may have—including the awareness of hues—must reside in the optic tectum. There is no 'higher' visual center in the fish brain. But there are connections of the tectum with other brain regions, some of which might be vital to visual associations. Nolte, however, working with *Phoxinus* and *Gasterosteus,* found that the removal of such of these regions as could be destroyed without killing the fish, failed to disturb the learning of associations with color stimuli. He extirpated in turn the cerebral lobes, the habenular ganglia, and the molecular layer of the cerebellum. The fishes still responded to color; and others, which were trained to colors only after such operations, learned in the normal time.

We might expect that even in the highest vertebrates much of visual consciousness, including perhaps hue-consciousness, would continue to be mediated by the homologues of the optic tectum, which are the superior colliculi. But in the evolution of the nervous system the superior colliculi have become very decidedly a spur track of the visual pathway, and are concerned only with relaying impulses for reflex and willed movement to the extra-ocular and other muscles (see Fig. 123, p. 335). We have seen (p. 336) that in man all visual sensations reside in the cortex, where color sensations are most susceptible of all to injuries of the visual area in the occipital lobe. In man, the lateral geniculate nucleus may play a considerable rôle in vision; but the optic tectum is purely a reflex center and has surrendered, to the geniculate and the cortex, any functions in visual sensation which it may have had in the fishes and amphibians. Although the teleostean and primate color-vision systems may be physiologically identical in their dependence upon three elementary central processes, it would seem that they must be very differently localized in the respective central nervous systems—in the optic tectum in the one, and in the lateral geniculate or in the cerebral cortex in the other. The location of color vision in the brains of reptiles and birds is a problem which has had no attention, though it should be susceptible of experimental attack.

In the detailed localization of the color-sense within the primate cortex, an interesting start was made a decade ago by the Swedish neurologist Henschen. He found that in layer IV of the visual cortex (see pp. 334-7 and Fig. 123) two different types of ganglion cells could be seen in species having duplex retinæ. Henschen identified these two types as

'light-cells' and 'color-cells', and believed them to have ultimate connections respectively with the rods and cones of the retina. Color cells were especially numerous in *Nemestrinus,* which has a fovea and has been shown to have color vision. They were sparse in *Lemur macaco,* which, though diurnal and provided with an area centralis (if not a fovea), probably has no more color vision than *L. mongoz* (*v.s.*). Color cells were entirely lacking in the pure-rod *Perodicticus potto,* which Henschen consequently suggested would prove to be the only primate, among those examined by him, entirely devoid of a color sense.

These investigations have never been carried further; but it would be most interesting to compare, for example, the layer IV's of diurnal squirrels and flying-squirrels—one might find that the two types of cortical cells represented rods and cones right enough, but not necessarily achromatic versus chromatic sensory capacity. More interesting still would be someone's demonstration of an analogous histological duplicity in the visual centers of some of the many sub-mammalian possessors of duplex retinæ, known either to have color vision, or not to have it.

(B) Dermal Color-Changes

No class of vertebrates is lacking in members which, from time to time, alter their color patterns by some means or other. There are vast differences from group to group as to the means employed, the length of time involved, the facility and frequency of the changes, and their biological values. The basic color patterns themselves, and those of animals which cannot change them at all, may or may not be demonstrably adaptive in particular cases. The somber colorations of strictly nocturnal mammals are almost certainly not, for they pass unseen anyway. But we like to think that the vertical stripes of a tiger help to hide him in a canebrake. Fishes are dark above and pale beneath, so that they blend with the bottom or with the bright water surface depending upon the point of view of the beholder. We feel sure that this pattern is adaptive—and feel convinced when we are confronted by such a phenomenon as the African catfish *Synodontis,* which swims upside down and whose reversed coloration is expressed by its Arabic name, 'batensoda' (= 'black belly').

To be sure, the theory of warning and protective coloration is in disrepute as regards any universal applicability; but there remains an unshakable residuum of evidence that concealing colorations exist and actually do protect. There have even been experimental demonstrations. In

Italy, there are both green and brown varieties of the praying mantis. In 1904, di Cesnola tethered 20 green mantids in green grass and 20 brown ones on some brown, withered grass. Seventeen days later, all were still alive. When he tethered 25 green mantids on brown grass, all had been eaten, by birds etc., eleven days later. Of 45 brown insects placed in green grass, 35 were dead in seventeen days. Similar experiments, with similar results, were made years ago by Poulton, Sanders, Crampton, Bumpus, Davenport and Weldon, and more recently by Carrick, Young, Gerould, and Isely.

Very recently, the protective value of *changeable* coloration has been shown experimentally by Sumner. When his fishes (*Gambusia*) were allowed to adapt to the shade of their background they were far less often caught by penguins, herons, and predaceous fishes than other individuals placed in tanks which they did not match. Certainly, adaptiveness of an animal's coloration is the more likely, the more that coloration is *altered* by the animal. If the alteration is adaptive, we must suppose that the pre-change pattern had been adaptive, and has ceased to be so under the conditions which produce the change. Sometimes—as in most lizards—the change has nothing whatever to do with making the animal less conspicuous. In such cases, we have a right to look for other ways in which the change may yet be interpreted as adaptive to some end or other.

Modes of Color Change—The warm-blooded animals are under strict limitations as to the changes they can possibly make. Their colorations reside in lifeless hairs and feathers. They can sometimes be altered quickly—locally—by skin muscles, as when a pronghorn displays his white rump-patches, or when a running antelope-jackrabbit turns white in its flight by revolving the belly skin up onto the side toward the pursuer and laying back his ears. But when a weasel or a willow ptarmigan prepares for winter by turning white practically all over, it is by the arduous growth of new, white hairs or feathers and the shedding of the old. One can cram a canary with foods rich in carotene, but the resulting golden-yellow color will appear in the plumage only after the next seasonal moult. Similar passive changes can be forced even upon man by manipulation of his diet, or by exposing him to the sun until, in self-defense against ultraviolet light, he becomes tanned by increased melanization.

The fishes, most amphibians, and many reptiles expose to view living pigmented tissues over the whole surface of the body. For some of these animals, color changes may be only seasonal, as in the adoption of a

special nuptial pattern for the breeding period. The changes may be local, as in the spreading of a lizard's throat-fan by engorgement with blood, which then shows red through the transparent skin, or in the blush of an excited macaw, which has a similar basis. But in large numbers of species, relatively rapid changes are made by the whole skin in sympathy with the time of day, temperature, humidity, or the shade or color of the background. Even the nuptial coloration can be put on or off at a moment's notice by some fishes, such as the cichlids and the red-bellied dace (*Chrosomus*). These rapid changes were first produced experimentally by Stark in 1830. They are possible because the dermal pigment, or a good part of it, is contained not in inert cells or in defunct or cornified tissues, but in active star-shaped cells. These were discovered and named

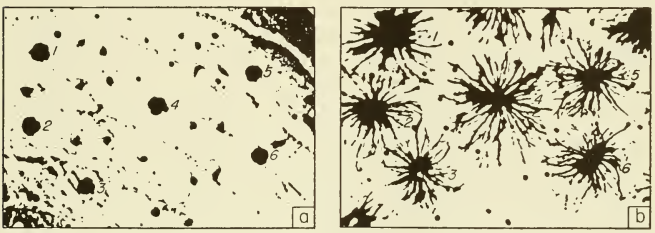

Fig. 157—Dermal chromatophores of *Fundulus heteroclitus;* identical chromatophores are similarly numbered in the two pictures. From Parker, after Spaeth.

a, contracted; b, expanded condition of pigment masses.

'chromatophores' by Sangiovanni in 1819; and in 1860 Kölliker, studying a lung-fish, *Lepidosiren,* first showed clearly how they work to change the appearance of the animal.

Only while they are developing do these chromatophores ever actually change their shape. In fully-formed chromatophores, the cloud of pigment granules within the cell may be swept into a compact mass by centripetal cytoplasmic streaming, or dispersed uniformly out into the arms of the 'star' by converse movements (Fig. 157). Expansion of the pigment masses of a given set of chromatophores gives their particular color (or optical colors which they influence) to the skin region in which the expansion occurs. The aggregation or contraction of the pigment masses makes of them minute dark dots in a pallid expanse of skin, lightening up the animal's coloration or giving some other class of chromatophores

a chance to affect it by expanding. Both the expansion and the contraction of the pigment mass appear to be active processes—neither is comparable with the relaxation of a muscle.

Chromatophores are of several types. Most widespread of all is the 'melanophore', containing the dark brown, almost black pigment melanin. The predominance of melanophores is largely responsible for the fact that dermal changes of *shade*, in an achromatic sense, are more widespread among species and more conspicuous in individuals than are changes of *hue*. This predominance probably indicates antiquity. Other types of chromatophores would seem to be newer inventions. Some of them operate quite differently from melanophores. In a particular species, one type may be changeable and another not; and in some animals (lizards, snakes) they are all quite inert so far as we can tell.

Some colored chromatophores, generically called lipophores because their pigments are fat-soluble carotenoids, take their special names from their colors: erythrophores (red), xanthophores (yellow), xantholeucophores (changeable from yellow to white) and so on. A third class is comprised by the iridocytes, which may be inert or active, free or associated closely with other chromatophores to form iridosomes. The pigment in iridocytes is the familiar guanin, which may give the cell a white or silvery color, or even produce an enamel-like yellow, blue, or green depending upon the way in which the platelets of guanin operate to produce interference between the wavelengths of light they reflect. A single iridocyte may, as in *Fundulus parvipinnis*, scamper through green, orange, yellow, and red phases in successive moments.

'Physiological' and 'Morphological' Chromatophoral Changes

Chromatophoral changes may have little to do with illumination, or they may closely adapt an animal to the shade of its surroundings, to the color of the background, or to both. In some species (as certain flounders) even the pattern can be roughly matched, as Sumner first showed in 1911. The fishes take on large blotches when over a coarse polka-dot pattern, small spots when on a small-dotted background. These rapid, transitory changes (not of pattern, however) were of course known to the ancients, and were described for the chameleon and invertebrates (cephalopod molluscs) by Aristotle. As early as 1882 Flemming suggested, on the basis of his experiments with salamander larvæ, that the actual number of chromatophores could be influenced by the surroundings of the animal. In 1909, Secerov coined some terms to express the distinction which his work on a fish (*Barbatula barbatula*) led him to

make: the quick changes he called 'physiological', the slower ones, requiring weeks or months and having their basis in an increase of the amount of pigment or the number of pigment cells, or both, he called 'morphological' color changes. These terms are not too good, for both kinds of change are equally physiological phenomena; but they have stuck. The very existence of morphological changes was questioned by reviewers right up to 1928, but in the past decade evidence for them has been piled up.

In 1910-1913 Babak, working with salamander (*Ambystoma*) larvæ, came to a conclusion which is now known as Babak's law: If the conditions for producing a given physiological color change are maintained for a long period, the corresponding morphological change will take place if it is within the capacity of the animal. Modern experiments, especially those of Francis Sumner and his co-workers at the Scripps Institution of Oceanography, tend to show that while Babak's law holds pretty well, the relationship it expresses is not a genetic one. Morphological changes are apparently not the direct result of the chromatophoral system's setting itself in a given state and holding that state—rather, the two kinds of changes have a common cause.

Control Through the Eye—This cause is always an intricate one, and varies from group to group of animals. Lister established in 1858 that in the frog the eye initiates the process of dermal change, and we now know that this is nearly always true. If the eyes of poikilochromic (*i. e.,* color-changing) vertebrates are covered or removed, no further responses to background—or at most only slight ones—occur. Responses to temperature, and to light and darkness, may however go on about as before.

The eye is thus not only the receptor for vision, and for a host of reflexes concerned with its own control, but it also mediates a reflex arc of some sort which ends in the dermal chromatophores. What constitutes the middle of the arc—whether nerve impulses or blood-borne substances—is another matter. Before considering that matter, it needs pointing out that for the eye to control dermal responses to its field of reception has no implications whatever for vision in that field. We need not suppose that for an animal to respond to a background, he must be visually conscious of its characteristics of hue and tone. As a matter of fact, the eye of a fish can adjust its melanophores to different neutral backgrounds whose difference in tone is too small for the same fish to discriminate visually in a training procedure! Of course in the work of Mast cited in the preceding Section, the instant choice of a particular background by a flounder adapted, dermally, to that background certainly had a basis in

whatever visual consciousness a fish may possess. More recently Brown and Thompson have shown that in eight species of freshwater fishes, individuals adapted to pale or dark backgrounds would prefer the respective backgrounds when allowed to make a choice. But the color changes mediated through the eyes are just as mechanically reflex as is the visceral disturbance we may experience from certain shifting patterns of visual stimuli which we cannot even recognize or describe.

Physiological Color Changes in Teleosts—Of all fishes—indeed, of all vertebrates—it is the teleosts which display the greatest versatility in both physiological and morphological changes of costume. And, it is these forms whose chromatophoral performances are most wholeheartedly devoted to fitting the animal to the pattern of its surroundings. Many marine forms, like the swordfish and tuna, do have relatively inert colorations. Very probably this is because, being pelagic, they are never near a substrate or background and have no need of a capacity for adjusting thereto. But many littoral fishes, particularly marine ones and especially the hordes of tropical coral-reef species and the rock-reef fishes of the temperate zones, can manipulate their colorations with real virtuosity, and may match their backgrounds closely. The groupers (genus *Epinephelus*) have been called the chameleons of the sea—which is a gross under-compliment since the true chameleons actually have less of a dermal repertoire than a tree-frog. Some of the flatfishes are not far behind the coral-reef fishes. The rapidity of their shifts of color as they glide over a variegated pattern has been called 'blush-like'. One Nassau grouper in a New York aquarium was observed to don eight radically different liveries within a period of a few minutes. Beebe has described a fish which he watched as it swam in amongst some coral and out again. When it went in, it was a shining blue with three vertical brown bands. When it came out a few moments later it was a brilliant yellow, thickly covered with black polka-dots—and Beebe was able to assure himself that it was really the same fish.

There are species in which portions of the whole color pattern reside in internal organs (peritoneum, meninges, etc.). These colorations show through to the surface owing to the transparency of the overlying structures, and are blended with patches of dermal color to form the overall pattern of the fish. This is the situation in *Coryphopterus glaucofrænum;* but in *Eviota personata* all of the color pattern is internal, the muscles and bones are transparent, and there is but little pigment in the skin. These internal colorations change in sympathy with, and in coöperation

with, the changes in the skin; but nothing is known concerning their immediate causation and control.

Mode of Control in Teleosts—The speed with which fishes can effect skin changes, together with the fact that they occur all over the body at once, speaks for nerve impulses; and in fact it is now generally believed that in all poikilochromic teleosts the nervous system is in practically complete charge as lieutenant to the eye. The work of Pouchet in 1876 was the first to indicate this. The cutting of nerves in turbots put out of action the chromatophores of corresponding skin areas. In 1893 Ballowitz demonstrated profuse nerve endings on the melanophores. Others since have been able to make out that these autonomic fibers are of two kinds, affording a double, reciprocal innervation. There is a little evidence that endocrine secretions—so nearly all-important in amphibian dermal changes—play a very minor part in teleosts. It has been claimed, though with insufficient proof, that posterior-pituitary extracts increase the amounts of melanin in teleost melanophores, and that the lipophores have no nerve supply at all and are entirely under pituitary control. The isolated melanophores of a single scale will respond to autonomomimetic and other drugs (though not to visible light), but this does not imply as much for a hormonal control in the intact fish as it may seem to do. We now know that nerve fibers arouse effector end-organs by means of secretions from their tips—the so-called 'neurohumors'; and that these latter include such substances as adrenalin and acetylcholine. Nervous and hormonal control-mechanisms may thus be said to have a common denominator.

It has been found that depressants of the nervous system, such as anæsthetics, produce an 'expansion' of the melanophores of *Fundulus;* while reflex paling results from the administration of stimulant drugs. The dermal changes of this much-studied fish are speeded up by increased temperature, and proceed at different rates under the different osmotic circumstances of fresh water versus salt; but these facts are not incompatible with the idea of nervous control. When a spinal nerve is cut, as Pouchet originally showed, the melanophores in the skin supplied by the nerve become expanded and remain so for many days, until the motor fibers of the nerve regenerate. Some slight and sluggish activity remains in the chromatophores however, even after their denervation, indicating that the ebb and flow of hormonal concentrations in the blood stream are not without some effect. Local interference with the circulation abolishes this residual activity, though this may be due more to the shutting

off of the oxygen supply than to a deprivation of hormonic stimulation. More significant, and suggesting a direct chemical influence of the retina itself, are the recent experiments of Szepsenwol. He transplanted the adult eyes of *Fitzroya lineata* to new locations in the body where they could have no connection with the nervous system, and found that the chromatophores would still perform.

Response to Albedo—The physiological dermal changes of the average teleost consist of simple darkening on dark backgrounds and paling on light or white ones. Both normal and eyeless animals become pale in darkness, but eyeless animals mysteriously darken in the light. In some species, as in the flounders lately examined by Osborn (*Pseudopleuronectes americanus* and *Lophopsetta aquosa*), the blinded fish takes on an intermediate shade, and the dark spots normal for the intact animal disappear—this being the pattern which the intact fishes assume in darkness.

It may seem odd enough that a blinded fish should respond to light at all, and we will consider the possible reason for this in a page or two; but there is an even greater peculiarity about the responses of the intact fish to light and dark backgrounds: it was Sumner who, years ago, first noticed that in these responses the intensity of illumination is of little consequence. This has been abundantly confirmed since, and has always seemed remarkable. If the fish were responding merely to the amount of light entering the eye, it should give the same dermal response to a brightly illuminated dark background as to a dimly illuminated white one—which would not adapt the fish at all! Instead however, the shade assumed by the skin of the fish is always (unless the intensity of the incident light is very low or extremely high) in accordance with the *albedo* of the substrate—the percentage of incident light which the substrate reflects.

A response to albedo sounds impossible. It would be like a response to specific gravity. The strange thing is that we do respond to specific gravity—in the so-called size-weight illusion, wherein a pound of lead is actually judged heavier than a pound of feathers. Analogous, also, is our ability to recognize a melody as 'the same' after transposition to another key.

These phenomena have their counterpart, in human vision, in the one which psychologists call brightness constancy. We see snow as white in the evening, and see coal as black in noonday sunlight, even though the

coal may be reflecting more photic energy than the snow had done. In some way, our perceptual machinery (not our thinking processes—it works too fast for them to be involved) makes allowances for the intensity of the general illumination. We can easily be led to see white paper as gray, or black paper as nearly white, if our clues to the overhead illumination are eliminated in an experimental situation. Similarly, the even more fully automatic 'allowance-making' mechanism of the fish can be deceived. If, by such devices as the use of translucent material lighted from below, the substrate is made lighter or darker than the overhead illumination would call for, the skin of the fish changes accordingly.

Sumner early suspected that this ability of the fish to adapt the chromatophores to background albedo was due to a vertical polarization of the retina. The retina was thought to control the pigment cells in sympathy with the *relative* illuminations of its upper and lower halves, corresponding respectively to the lower part of the visual field (the substrate) and the upper part (the source of natural light). Von Frisch soon produced experimental evidence for this view, to which Sumner and others have since added a great deal.

By means of vaseline-lampblack paint, and by fitting celloidin caps, blackened in various patterns, over the corneas of fishes, Frisch and Sumner have shown that when the upper half of the cornea is left clear and the lower half blacked out, the fishes will darken greatly regardless of the tone or albedo of the substrate. If only the lower cornea is clear, pale-adapted fishes remain pale on either white backgrounds or dark gray ones. All-black covers did not always prevent all shade-changing ability, probably because light could still reach the retina through the translucent tissues of the head. Ordinarily, however, fishes so provided darkened up as though they were eyeless. In the entire situation, then, we can see certain tendencies:

A. When no light is striking the fish (with or without its eyes), the melanophores 'contract'.

B. When light strikes only the skin (whether the eyes are present or not), the melanophores 'expand'.

C. If more of any light entering the eye strikes the upper part of the retina, the melanophores 'contract' despite Tendency *B*.

D. If more of the light entering the eye strikes the lower part of the retina, the inhibitory effect of Tendency *C* upon Tendency *B* is ineffective, and the melanophores 'expand'.

Thus in the ocular control of dermal response to the shade of the background, the upper half of the retina acts positively to contract the chromatophores, and the lower half of the retina acts in a negative way to prevent such contraction. A blinded fish darkens in the light because there is no eye to inhibit the innate tendency of an illuminated melanophore to expand. In other words, *C* (above) becomes impossible.

Frisch found, in trout, that blacking out one eye led to a darkening of only one side of the fish—the opposite side, because of the total decussation of the optic nerve fibers in the chiasma (Fig. 21, p. 47). Sumner did not find this response in the species with which he worked. A fish with one eye covered took on a shade intermediate (for a given background) between a normal fish and one with both eyes covered. Either eye ordinarily can control all of the melanophores, which seems to demonstrate an interesting phase of binocularity in piscine ocular physiology: despite the total decussation of the optic nerves, each retina has connection within the brain with both halves of the central nervous system. The unilateral response in the trout (and other fishes) seems to be the best kind of evidence for nervous control of the melanophores. No hormone could very well remain only on one side of a vertebrate's body.

Various attempts to confirm and study the 'polarization' of the retina by inverting the illumination, rotating the fish, or destroying either half of the retina have been successful. Not so, most efforts to rotate the eye of a fish 180° in its orbit without killing the animal. Butcher, however, has succeeded with this operation in *Fundulus*, and finds that the fish will then give its tawny response to a yellow background only when the latter is above the animal.

In general, dermal responses to *hue* exhibit no polarization at all. That is, no contrast between the upper and lower parts of the visual field is required. This seems particularly interesting when one recalls the contention of some workers, that the colored chromatophores of fishes are not controlled through the nervous system. Sumner got the same yellowing of his fishes when corneal caps were applied whose upper halves were yellow, black, blue, or clear—so long as their lower halves, admitting the light reflected from the white substrate, were yellow. With an all-red covering, the fish took on the same dermal color as when in a red container with its corneæ naked.

Morphological Color Changes in Teleosts—At the present time it is the morphological color changes which hold the stage of interest. Occurring in the same directions of darkening and paling, under the

same conditions as the evanescent physiological changes, their causational chain of events is not yet wholly clear. They appear to be usually under the ultimate control of the eye, though when flounders are illuminated from below and proceed (after many months) to acquire active chromatophores of all sorts on their erstwhile snow-white undersides, it is sometimes hard to see how the eyes could have been responsible. Not all flatfish species have their eyes raised on any sort of 'turrets', so that they could possibly see the substrate. It is difficult to imagine how year-long streams of nerve impulses can evoke chromatophores from the mesodermal nowhere, or cause them to vanish entirely. And, the increase in the number of melanophores of an illuminated, eyeless, fish is as much of a mystery as is the physiological darkening of such fishes by light.

The commonest morphological changes in teleosts occur outside of laboratories. Aquarists have long fretted over the fact that some of their most gorgeous prizes soon become drab in captivity. The loss of glamor can often be forestalled by careful attention to the diet; for a goodly part of dermal matching-of-environment is really quite automatic, due to the fact that the fish acquires many of its pigments directly by eating the flora and fauna of his immediate environment. To a certain extent, the fish can't very well help taking in some of the very colors which surround him!

When a fish is kept for a long time on a dark or black background, the actual number of melanophores increases and the total amount of melanin extractible from the fish (and, perhaps, per melanophore) also increases. Concomitantly the guanophores decrease—at least, the amount of extractible guanin is reduced. Kept for weeks on a white ground, the fish will increase its guanin coating and will decrease the number of melanophores. Just what happens to these we do not know, though Ogneff thought they were phagocytized, eaten up by wandering tissue cells.

Blinded teleosts, and amphibians too, usually lose melanophores when kept in the dark. This fact has been used to account for the absence of dermal pigment in (permanent) cave-dwelling vertebrates, all of which belong to these two classes. Eyed animals of course also become depigmented in darkness, but eyeless individuals do not remain pallid when brought into the light. Their melanophores not only quickly expand, but soon begin to increase in numbers—not, however, if the pituitary gland is removed along with the eyes. Minus its pituitary, an eyed or blinded fish proceeds to lose melanin. Hilton found that adult *Typhlogobius,* which are normally eyeless and unpigmented (p. 388), would

develop chromatophores on the head if kept in the light for several months. Kurz has found that larval flatfishes (*Pleuronectes*), placed in the dark, cease to form any more melanophores and never develop lipophores at all. He also found that in these fishes (but not in the pike, *Esox*) white and short-wave lights stimulated the development of all the pigments while red, yellow, and green lights retarded them.

Abramowitz has reported that in *Fundulus majalis* the number of xanthophores increases within two to six weeks when the fish is kept over yellow or black substrates, decreases when the animal is over blue or white grounds. Sumner and Fox, however, found that in *Girella* the amount of xanthophyll extractible was greater in black individuals from black surroundings than from yellow fishes assayed after a sojourn on yellow or gray. Actually, there had been no gain in xanthophyll in the black fishes—only less of the *loss* which in *Girella* ordinarily occurs in the laboratory anyway. However, some of Sumner's recent work has indicated that fishes can deposit more xanthophyll in the skin than is accounted for in the food supplied to them. This hint, that fishes can convert carotene into xanthophyll, is borne out by the work of Lönnberg on Swedish marine fishes. Lönnberg finds only xanthophylls, no carotenes, in the skins of certain fishes which feed upon crustaceans *lacking* xanthophyll (but possessing carotenes) in their own pigmentations.

As with his demonstration of the response to albedo in physiological adaptation to substrate tone, so also Sumner has found an analogy for a visual phenomenon at work in the morphological changes of teleosts. In *Gillichthys, Gambusia,* and *Lebistes,* counts of the number of melanophores per unit area, or determinations of the amount of melanin in the skin, showed that the increase of pigmentation was inversely related to the logarithm of the albedo of the substrate. It was not surprising that the albedo should prove so important, and the intensity of the incident light a minor consideration; but the mathematical character of the relationship was unexpected.

Sumner has advanced the suggestion that this aspect of the morphological changes is in line with Fechner's modification of 'Weber's law'. The latter is a battered old psychological dictum to the effect that if, in any sensory modality, two stimuli differ quantitatively just enough to be perceived as different, their objective difference expressed in per cent is a constant. For example, if a five-pound weight and a six-pound one can just be told apart by heft, one is 20% heavier than the other, and any two weights must then differ by 20% to be discriminable. Fechner be-

lieved that the threshold of difference was not a constant percentage increment, but rather that it varied as the logarithm of the magnitude of the stimulus.

In psychological phenomena, Fechner's (or Weber's) law breaks down with both high and low values of the stimulus, but holds fairly well for a long intermediate range of values. So, Sumner finds, does the logarithmic relationship of increased pigmentation and albedo. Whether or not this phenomenon is an instance of the operation of Fechner's law, it is difficult to say. But when the control of the adaptive alteration of the protective colorations of vertebrates was originally delegated, logically enough, to the eye, it was also fairly logical that the eye should proceed to administer this particular physiological territory in accordance with the laws governing its own operation as the receptor of the visual sense —even though visual consciousness plays no part in the processes of color-change control.

Color Changes in Amphibians—Lister's pioneer work suggested that the dermal changes of the Amphibia are nervous reflexes. This idea was supported by Babak in 1910-1913, and in fact was quite generally accepted up to about 1924. The physiological changes of a frog between its pale and dark phases may take hours, or a day or more, to accomplish. In some tree-frogs, a few seconds may suffice. Morphological changes can be induced by experimental illuminations, and are particularly susceptible to dietary manipulation. These changes are of course a matter of weeks or months, as in teleosts. Such slow actions hardly look like performances of the nervous system. Yet if the eyes are removed, or the optic nerve cut, the changes in response to illumination are largely inhibited.

In 1898, Corona and Moroni found that injections of adrenal extracts would blanch a frog. Lieben rediscovered this reaction eight years later; and from 1922 on, Hogben and his colleagues argued for an almost strictly hormonal intermediation between the eye and the 'pigmentary effector system' of amphibians. As long as adrenalin was the only endocrine substance known to affect the phenomena, there was still room for the nervous system as the centerpiece of the picture; for the association of the adrenals with the sympathetic nervous system was well established.

But Hogben found that extracts of the intermediate lobe of the pituitary would darken frogs; and he came to believe, from further experiments, that a blanching hormone was produced by the pars tuberalis of the same gland. Much of this work was done on the primitive African clawed frog, *Xenopus lævis*. In this country the studies of Parker and

others on the local *Rana pipiens* indicate that in this frog only one pituitary hormone is involved, not two. Blood serum from dark *pipiens,* injected into pale ones, will darken the latter; but interestingly enough pale-frog serum fails to blanch dark frogs. Adrenalin injections, or the removal of the pituitary, will produce a more complete paling than will the bright illumination of a normal frog in white surroundings. Frogs whose pituitaries have been removed will, in time, lose much of their pigment—a 'morphological' change. Experiments similar to those of Szepsenwol (p. 530), designed to test whether the eye itself secretes skin-controlling hormones, have yielded conflicting evidence in amphibians.

In amphibians the color-changes are less widespread and conspicuous, as well as less rapid, than in teleosts. Few have any greater repertoire than the brown-green-cream series of phases in the common tree-frog *Hyla versicolor.* Not only is the control largely (sometimes, wholly) hormonal instead of predominantly nervous (except in a few tree-frogs), but the authority of the eye has begun to dwindle, approaching the situation in lizards. In some forms, as for instance the common newt (*Triturus viridescens*), the pattern of the adult shows no measurable changes toward photic stimuli, though darkening will occur at low temperatures and paling can be induced by pituitrin. Response to background does occur in many species, but only when temperature and humidity conditions permit—a conjunction which is so far from being the rule that it is almost an accident. When a frog is caught in the daytime amid green grass, and happens to be green in color, it is in a sense a coincidence. At a lower temperature, the frog would have been brown. So also, if the grass had happened to be wetter. The frog can blend with its environment only when three factors are just right: light, temperature, and moisture. The eye can aid the response to only one of these factors, *i. e.,* light. In teleosts, the eye is able to control the skin largely because temperature and humidity do *not* control it. But at least amphibians are able to attain the pale phase (appropriate to bright light and backgrounds of high albedo) at moderate temperatures—in contrast to the situation in most lizards, which can take on their pale phases only at relatively high temperatures.

Even tactile stimuli may have an influence. The European tree-frog, *ceteris paribus,* will turn brown on a rough surface and green on a smooth one. In a roundabout way, such changes are perhaps adaptive to background, for the brown bark of a tree is rough, and the green leaves are smooth.

In still other ways, the amphibian phenomena differ from those of teleosts. Blinded frogs, like normal ones, respond dermally quite independently of light and darkness in situations which are warm and dry or cold and wet. At moderate temperatures, in the presence of adequate moisture, the melanophores of eyed frogs contract in bright light and expand over dark backgrounds. But in darkness they also expand, instead of contracting as in fishes. Blinded frogs expand their melanophores in darkness, and these will contract only to a tiny extent if the animals are then illuminated. However, Laurens found that in larvæ (*Ambystoma*) the reactions of blinded individuals were like those of blinded teleosts, though markedly retarded as compared with normal larvæ. The primitive tendency of melanophores (as shown in teleosts and in young amphibian larvæ) is, as Parker has pointed out, to expand in the light and contract in the dark. With age, the eye comes to be able to inhibit the expansion in the light; and, in amphibians, the presence of the eye—if in its normal location, at least—somehow causes or permits the melanophores to expand in the dark.

By and large, the dermal color-changes of amphibians are nowhere nearly so clearly adaptive to background as those of teleosts. This is even more true of the lizards. Darkening in low temperatures, and blanching at higher ones, are such predominant activities that Max Weber was prompted years ago to suggest that in both amphibians and reptiles the dermal changes are designed primarily to regulate the temperature of the animal, by adjusting the light-absorbing capacity of the skin. We will consider this theory shortly when we come to the reptiles.

Dermal Changes in Lower Fishes, and 'Diurnal Rhythms'—The seemingly paradoxical physiological kinship of the Amphibia and the elasmobranch fishes, manifested in various other ways, is also borne out by the character of color-change control. Color changes in elasmobranchs went unnoticed until less than a decade ago. These fishes are generally grayish or neutral in garb; and though they are sometimes stated to have no typical melanophores, they are capable of changes in shade. The eye operates these changes by way of the pituitary in all the investigated species except one, wherein the blanching process (though not the darkening) seems to be under the direct control of the nervous system. No morphological changes are known to take place in elasmobranchs.

We do not know much about color changes in other 'lower' fishes. At least two of the three lungfishes (*Protopterus* and *Lepidosiren*) have them, but their operation has not been investigated. In 1935 Young

found that in lampreys (*Lampetra*), the dermal changes are mediated through the pituitary and not through spinal nerves, and that the median eyes (see p. 339) share in the control of the changes, along with the lateral eyes.

Lampreys, Young found, become paler at night, darkening in the daytime—and keep up these changes for many days when kept in constant darkness. Similar intrinsically rhythmic changes were reported in 1926, by Pauli, for a teleost (*Phoxinus*), where they were very slight, and for larvæ of *Salamandra maculosa,* in which they persisted for about a week. Slome and Hogben, in 1929, reported marked rhythmical changes in an anuran (*Xenopus lævis*) kept in the dark.

Such diurnal rhythms, which occur also in the retinal pigment cells of some fishes (perhaps also in frogs), are inherent, and outside of the control of the coloration by the photic stimulation of the eyes. Whatever their cause, it is suppressed by light. No vertebrate exhibits any rhythmical dermal changes when kept illuminated night and day.

Color Changes in Reptiles—Despite the reputation of the chameleon for being able to match any colored background (and its alleged tendency to suicide when placed upon plaids), it can be asserted that no reptile dynamically adapts its skin primarily to the background. The dermal response to the character of the light entering the eye, or to bright light in bright surroundings, *may* suit the animal's pattern better to the background; but any such improvements of concealment are even more completely fortuitous than they are in amphibians.

It is only in lizards that conspicuous changes occur. Even among the lizards there are only a few families which show chromatophoral changes well—notably the Agamidæ of the Old World and their counterparts, the Iguanidæ, in the Western Hemisphere; and of course the Chameleontidæ. The only changeable pigment cells are the melanophores, which in most reptiles underlie the iridocytes but, in poikilochromic forms, send the pigment up into cell-branches which are intertwined with the varicolored iridocytes.

To no lizard has the *color* of the background any significance. A response to hue is made in a curiously indirect way, however, by *Anolis carolinensis,* the 'Florida chameleon' (which is really an iguanid). Responses to light and darkness by paling and darkening are about as in the teleosts, but they are even more at the mercy of temperature changes than in amphibians. Each individual lizard has a light phase and a dark phase. Wherever a species seems to have a great variety of costumes (as

in true chameleons) it is due to individual variation. Thus particular chameleons of a single species may vary, in their pale and dark phases, between green and dark brown, yellow and olive, buff and black, etc.

The melanophores react to temperature as in the amphibians, expanding at low temperatures and contracting in high ones. In general, while contraction will occur in amphibians at average outdoor temperatures, in lizards the temperature must be rather higher before paling ensues even in bright light. If the lizard happens to be a desert form and, after paling in the heat of the sun, blends fairly well with the sand, we may call this adaptation to background if we stretch a point. Actually however, Max Weber's idea seems pretty sound where lizards are concerned. By paling at high temperatures (which ordinarily means in the sun), and darkening at lower ones, they can reflect light (and heat) when they are already well warmed, and absorb a larger proportion of it when the absolute amount available is less. No useful purpose, in connection with heat-conservation or anything else, seems to be served by the paling which takes place in darkness, however. Here, probably the ancient proclivity of melanophores to contract in the dark is only asserting itself, and we need not seek any ulterior explanation.

The lizard's responses to high and low temperatures are direct reactions to temperature. But we may, if we like, take the attitude that they are biologically intended, so to say, as responses to the accompanying light and darkness: bright light, in the environment of a lizard, means high temperature; dim light or darkness connotes the cooling of twilight and nightfall. Here we have an analogy for the effect of substrate texture upon the European tree-frog (*v. s.*).

Light and darkness, as such, are effective only within a restricted range of temperature. Within this range, the similarity of the behavior of lacertilian and teleostean melanophores is striking, as Sand pointed out a few years ago. They contract on white backgrounds and expand on black; they contract in darkness in both normal and eyeless animals; they expand in eyeless animals upon illumination of the body; and they expand in any denervated area of the skin. Blindfolded animals, unlike eyeless ones, remain dark upon lighted backgrounds, showing some inhibitory influence of the eye; but this influence is readily masked by that of temperature or excitement.

The response to denervation is but one of a number of indications that the eye exerts its control through the nervous system. The responses to temperature, however, are of doubtful mediation. Like those to light,

they go fast enough to make nervous control seem reasonable—much more so than in most amphibians. The consensus, however, is that in lizards the principal controlling mechanism is an antagonism between adrenalin and a dispersing hormone produced by the pars intermedia of the pituitary.

The response to excitement is particularly prompt, but it is unquestionably entirely endocrine. This response is given by lizards to any noxious stimulus, a number of which—electrical stimulation of the mucous membranes, for example—are used experimentally to induce the so-called excitement pallor. Its appearance is very regular, but may be suppressed by low temperatures. The blanching has been abundantly proven to be brought about by the adrenals. It occurs even in denervated areas, indicating that the influence of adrenalin is direct, and that the adrenalin or adrenalin-like substance involved is not a neurohumor, secreted in tiny amounts by nerve fibers ending in the chromatophores. Hadley, however, doubts the direct action, on the basis of his 1931 experiments on bits of excised *Anolis* skin. While the melanophores of such bits would respond directly to illumination, showing them to be apparently normal despite their isolation, direct applications of strong adrenalin expanded them—whereas the same solution injected into an intact animal produced the usual wholesale contraction and pallor. Pituitrin expanded the pigment cells both in intact lizards and bits of skin.

Local effects have also been produced in the intact animal. Redfield, working with the horned lizard *Phrynosoma,* found that local heating of the skin (light being excluded) would contract the melanophores without affecting those elsewhere. Local illumination is also effective as a stimulus, but produces expansion—which cannot here be due, like so many supposed biological effects of light, to a heating action of the light. But this apparently paradoxical expansive effect of heatless light does tie in with some of the findings of Sarah Atsatt, whose recent paper on desert lizards may sometime be called a classic:

Miss Atsatt so designed her apparatus as to divorce temperature from light, and make each independently variable. Her findings tend to explode some hitherto well-rooted ideas, but they were so different for different species that only further work along the same line will show just which of our smug generalizations (some of them stated above) must be discarded. In thirteen iguanid species and one gecko, the response to high temperature (35-43°C) was the light phase; and to low temperature, the dark phase. One species, *Callosaurus ventralis,* became partly pale again

quite regularly, as an afterthought, after some time in low temperature. Among the forms she studied, the one which was most active in the winter was *Uta stansburiana stejnegeri;* and this species took on its pale phase at a temperature as low as 25°C—a behavior comparable with that of amphibians.

Seven of the iguanids became pale in darkness and dark in the light (at moderate temperatures) but five species showed no differences in light and darkness, being obedient only to temperature. Two species of *Xantusia* available to Miss Atsatt responded to both light and high temperature with the *dark* phase, and would not take on the pale phase consistently in either low temperature or darkness. In the light of the nocturnality of *Xantusia,* we might cudgel our brains for an interpretation of this peculiarity—except for the fact that Miss Atsatt's one gekkonid species, *Coleonyx variegatus,* is just as nocturnal, and yet becomes pale in high temperature and in darkness, and darkens in low temperatures and in illumination.

An influence of hue upon the dermal responses of a lizard (*Anolis carolinensis*) has been shown by the interesting preliminary experiments of Wilson. This 'Florida chameleon' is the little chap sold at circuses, with the disastrous advice to feed it on sugar-water. It is usually hawked while tied to a board covered with green baize, and the pitchman is careful to keep in the shade—else the animals cease to 'match' the board, and turn brown. This is the whole gamut of the animal's changes—from green to brown; but it does truly equal that of its African namesake.

Wilson fitted green cellophane covers over the eyes of the lizards, and covered some glass jars with similar material. He found that the green phase was always produced by darkness, the brown phase by bright light. Any brown individual, placed in a green jar, became green. Green cellophane over the eyes induced the green phase. If the eyes were blacked out, either white or green light induced the brown phase. If one eye was covered with green cellophane and the other with black, the green phase was assumed as perfectly as if both eyes were acting. A few animals with green hoods, and in a green jar, became intermediate in phase (yellowish brown); but Wilson noticed that they seemed sluggish and were blinking their eyes—hence it was only natural that they should be intermediate between the expected green phase and the brown one which they would assume upon closing the eyes for an even greater part of the time with the body exposed to light.

These fascinating results help to explain why this lizard, which *can* turn green and disappear when it is on a background of foliage in its native haunts, does not always do so. Green light can stimulate the retina to evoke, through the nervous system, a green body coloration; but any light—even a green one—striking the body strongly, only leads to melanophore expansion and the onset of the non-adaptive brown phase. If there are any photoreceptors in the skin, they are unfortunately not specifically responsive to green light.

Wilson points out that when *Anolis* is among leaves and the eyes receive light filtered by other green leaves overhead, the green phase ensues. The animal is then adapted to its background—though not, as a teleost would be, through the character of the light reflected from that background. But let the lizard come out from cover, still standing on a green leaf, and the reception of light on its skin quickly turns it brown and causes it to stand forth like the proverbial sore thumb. Despite the interesting demonstration of a specific response of the oculodermal mechanism to green light, it seems over-charitable to credit this one reptilian species with an adaptability to background in the teleostean sense of the expression.

Color-changes have been reported in snakes from time to time; but, apart from some authoritative-looking old claims by Leydig for *Natrix natrix,* it is probable that all gross changes (particularly those in green tree-snakes mentioned by Fuchs) are caused not by chromatophoral alterations but by a spreading of the skin, revealing areas between the scales. *Dryophis,* in the anterior part of the body, exhibits a startling change of this character when excited.

Very recently Rahn has demonstrated that the dermal and epidermal melanophores of rattlesnakes, and the epidermal melanophores in three colubrid genera, will contract permanently if the pars intermedia (or the whole pituitary) is removed. Injections of 'intermedin' expand the chromatophores once more. Whether light and temperature alter the skin color in any of these snakes (by way of the eye or otherwise) is not known; but it is unlikely, inasmuch as the superficial layers of the epidermis—those due to be shed at the next ecdisis—contain a pattern of motionless pigment which conceals the activity of the melanophores beneath. The paling of the body, produced by removal of the pituitary, manifests itself only after the next subsequent moult.

The only other reptile in which melanophore activity has been demonstrated is the alligator. Kleinholz has found that the pigment in scat-

tered cells on the under surface of young specimens expands on black backgrounds and contracts on white ones. Pituitary and adrenal extracts respectively produce the same changes in the cells. It does not appear, however, that these phenomena can have any biological value—they do not occur on the visible parts of the animal, and may be absent in older individuals. The long-standing nocturnality of the crocodilians seems to account well enough for the vestigial condition of their color-changes. It may seem more surprising that the snakes, with such close taxonomic and ecological affinities with the lizards, should show so little evidence of dynamic adaptation to their surroundings. But this explains itself when it is considered as a part of the evidence for a lengthy subterranean sojourn of the earliest ophidians (see Chapter 16, section D).

(C) Coloration of the Eye

Basis of Iris Colors—The color of the eye itself presents some interesting problems—histological, optical, and ecological. Ordinarily, only the iris is involved. The pigment of the iris epithelium may be the only coloring matter present (p. 16), but nearly always there are stromal pigment cells containing various amounts of melanin, colored oils (iridocytes), or guanin and related substances which yield metallic appearances of silver, gold, or colors. As often as not, the coloration of an iris is the resultant of both pigmentary factors and such optical phenomena as interference. A vivid color may result from the absorption, by superficial layers, of some wavelengths and the differential reflection, by underlying tissues, of only certain ones of the remaining wavelengths. In this way, the green spots of a frog's skin and the blue iris of a Siamese cat are produced, without respective green and blue pigments being present at all.

Possible Significance—In our thinking about the possible meanings of eye colors, it is important to distinguish between pigmentation and coloration—these terms having respectively quantitative and qualitative connotations. Clearly, it is necessary for the pigments of an iris to absorb or reflect the greater part of the total illumination striking it. Bright pigments may contribute as much (or more) to the opacity of an iris, by reflection, as dark pigments do by absorption. But the pattern of colors the iris presents to the outside world is largely independent of the reflection-coefficients, or the amounts, of the pigments present. In short, a given blue iris may reflect the same amount of light as a given red one. Why, then, should one animal have the blue, and another, the red?

Apart from the possible mirror-action of silvery fish irides (see p. 238), there is no conceivable way in which the coloration of the iris can affect the vision of the animal, except perhaps at the very border of the pupil where the presence of brightly reflective material should theoretically be detrimental (though a metallic ring at the pupil's edge is extremely common in the lower vertebrates!). If iris colors in general have any explanations, these must be in terms of the interpretations offered for the body colorations of animals. A given iris pattern, then, might: (*a*) be intended to conceal the eye; (*b*) be intended to make the eye conspicuous; or (*c*) mean little or nothing.

Conspicuousness of the Eye—Many a writer on the subject of the adaptive coloration of animals has dwelt upon the conspicuousness of the eye and the means employed to abolish it. Three things tend to make the eye stand out on an animal, so that potential prey and enemies may discover the animal by noticing its eyes, even though the rest of the body may be well camouflaged. These three things are: (*a*) its roundness; (*b*) the blackness and roundness of the pupil; and (*c*) its glisten, due to its wetness.

Cott's clever drawing, reproduced here as Figure 158, shows strikingly how a round object set among other, even larger (but irregular) objects, takes the attention of the beholder. A species of animal may so arrange its coloration that the roundness of the eye is concealed. It is even possible to do something about the roundness and blackness of the pupil. But there is no conceivable way of eliminating the glistening of the cornea—though it eliminates itself under water, of course, in aquatic and amphibious forms. All three of these causes of conspicuousness, it is interesting to note, are employed in the 'warning' false eye-spots seen on the wings and elytra of many insects, and also in fishes (*e. g., Chelmon rostratus*) and toads (*e. g., Mantipus ocellatus*). Such spots are round, black-centered, and are often even high-lighted to give the appearance of glistening.

Concealment of the Eye?—The enthusiasts (*e.g.,* Cott) say that the color of the iris often matches that of the head as a whole. This is true enough, and yet it is no evidence for a concealment function; for, aside from the coincidence of silvery irides and silvery skins in many fishes, it is true only of nocturnal and crepuscular vertebrates, and not of all of them by any means. The crocodilians, for example, all have conspicuous buff or yellow eyes, and yet their bodies are very dark or even black.

The strongly nocturnal oil-bird (*Steatornis*) has bright blue eyes, and most owls have yellow ones.* Most wild mammals are dark brown or dark gray, and their irides are almost always of some shade of brown—small felids being quite exceptional with their metallic green. Under scotopic conditions, favored by most mammals, it will not matter a particle, for the concealment of the eye, whether the iris matches the body in color or not, so long as the two are roughly matched in tone or albedo. But the same, standard, dark brown mammalian iris occurs also in light gray

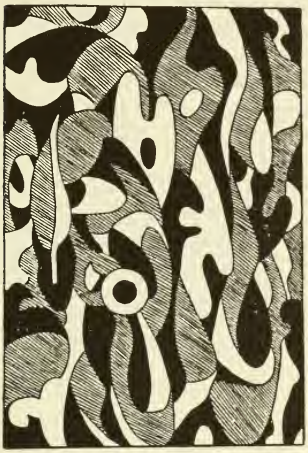

Fig. 158—"Diagram illustrating the inherent conspicuousness of an eye-spot, which attracts attention to itself in preference to a variety of other, and even larger, objects in the visual field" (Cott).

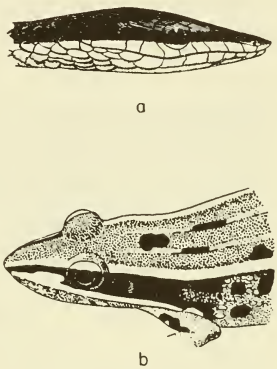

Fig. 159—Eye-masks. After Cott.
a, *Oxybelis acuminatus.*
b, *Rana sphenocephala.*

diurnal monkeys and squirrels—which is reason enough for thinking that the dark iris of a dusky and nocturnal mammal has no standing as an adaptation for concealment. Again, most salamanders have dark brown eyes, yet many of them have gaily colored bodies.

Among those vertebrates which are much out where other animals can get a good look at them—that is, the diurnal and arhythmic ones—it is highly exceptional for the iris to be unicolor, and a match for the head

*So also the nocturnal bat-eating hawk, *Machaerhamphus alcinus.*

skin. In birds and lizards, particularly, there seems to be rather a tendency to make the eye as contrasty as possible, and to employ it as a decoration! But some representatives of nearly every class of vertebrates bear markings which are supposed to be intended to conceal the eye:

These are such things as 'masks' and stripes of the head pattern which continue unbroken across the conjunctiva and iris (Fig. 159). The eye-masks of some fishes, frogs, and snakes are wide dark stripes passing horizontally (or, in fishes, about as often vertically) across the eye, which then loses its roundness since it is wholly 'absorbed' into the stripe. The mask may not include all of the eye; but if the pupil is included within its border, it is believed to serve just as well. Some masks are certainly fortuitous—for instance, Cott figures an antelope which has a black cheek-stripe sweeping up through the eye. Since a similar stripe develops from the eye through the crumen to the jaw in an adult Hampshire sheep (where it cannot possibly have any adaptive significance) such markings in mammals must be viewed with suspicion from our present standpoint.

More convincing, by far, are the instances where several *fine* stripes in the head coloration pass unbroken over the conjunctiva and iris. Unfortunately for any general acceptance of eye-concealment, such cases of so-called coincident disruptive coloration of the eye are excessively rare. Really good ones are such teleosts as *Pterois volitans, Labrisomus nuchipinnis, Ogcocephalus cubifrons,* and *Scorpæna plumieri;* and young specimens of our common painted turtles (genus *Chrysemys*), in which several black and yellow lines cross the eye (Fig. 160). The pattern in *Chrysemys* is closely imitated by that in the teleost *Apogon maculatus.* Ida Mann noted a similar situation in one other turtle (*Clemmys caspica*) and in one newt, *Triturus torosus;* but both of these examples are inferior to *Chrysemys.*

It is claimed that the goatsuckers and frogmouths (and a couple of lizards) close the eyes almost completely, as a means of concealing them, when danger threatens. This action might also be expected in their close relatives, the owls—who have so much more to conceal, since their irides, though sometimes black, are most often a vivid yellow or orange.* But

*In one—*Athene noctua*—such a performance would only make the eye more conspicuous; for, though this owl has yellow irides, it has white lids. In the daytime, owls have their eyes closed (to conceal them?—or in sleep?) particularly when danger is *not* threatening. The usual daytime photograph of an owl shows the eyes wide open, but this is because the photographer has disturbed the bird. A truly natural picture of an owl huddled against a tree-trunk (in its 'hiding' posture) always shows the eyes closed.

the owls do not have the habit. The narrowing of the lids *in an emergency* is open to an utterly different interpretation: it may well be a device for momentarily sharpening vision to a maximum, by employing the lid opening as a stenopaic slit. Myopic humans do the same trick—indeed, the very word 'myopia' is derived from roots which mean 'to shut the eye'.

Related to the above matter is another claim of the enthusiasts: that the best cases of eye camouflage, by masks and stripes, are seen in lidless vertebrates. *Pterois* is lidless; but *Chrysemys* is not. But this and other turtles, *Triturus torosus*, fishes, and snakes do have something in common to which attention has not been called. The eyes of aquatic forms, lidless or not, have no glisten when under water; and the snake spectacle

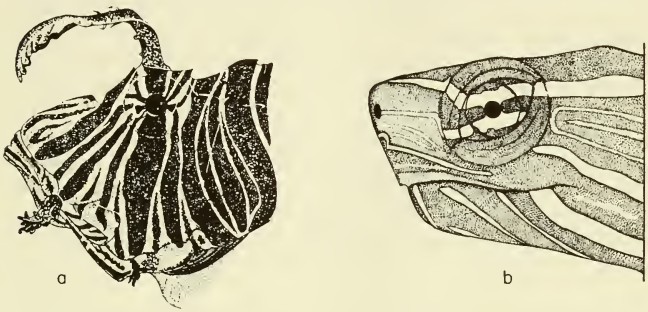

Fig. 160—Coincident disruptive coloration of the iris, conjunctiva, lids, and surrounding skin.

a, head of a lionfish, *Pterois volitans*. After Cott. b, head of the western painted turtle, *Chrysemys picta marginata;* drawn from life.

is so quickly dulled after a shed that the snake eye seldom has the luster of that of a bird or mammal. It may not be lidlessness as such, but the absence of glisten, which has made it worth-while for these particular vertebrates to devise camouflage for their eyes.

Glistening eyes, on the other hand, simply cannot be successfully concealed. It almost seems as though the birds and lizards, realizing this, have gone to the other extreme and have deliberately used the eye as the centerpiece of their fanciest decorations. Consider the guano cormorant, *Phalacrocorax bougainvillii*—it has a sober brown iris, but the naked skin around the eye bears a green ring next the eye, and a red ring out-

side of that. The proponents of adaptive coloration do not tell us why so many species of vertebrates—fishes, lizards, and birds with bright-colored irides; anurans, lizards, and cats with metallic ones—should advertise their eyes, particularly when so many of these very same animals have their bodies 'concealingly' colored. The nocturnal animals on which cats and owls prey do not, of course, see their enemies' irides as colored; but even so, the green of the cat's eye and the lemon iris of the owl would assuredly be seen as light-toned spots, even by an animal whose own vision was completely achromatic.

The difficulty of concealing the little black eyes in transparent fish larvae has been discussed previously (see pp. 237-8). Partial success may be attained by a precocious development of the silvery argentea layer of the chorioid, just within the transparent sclerotic envelope. A situation in one genus of batfishes, *Lophiomus,* to which Dr. Hubbs has called the writer's attention, serves to emphasize most strikingly the fact that the eyes of baby fishes often serve as a label, saying all too plainly: "Here is food." The batfishes are related to the anglers, and like the latter they are flattened dorsoventrally, with cavernous mouths over which, in the various species, there are suspended various sorts and sizes of 'illicia', or baits. The illicium dangles from a fishpole, rooted on the animal's back, and serves to lure small fishes within reach of the maw beneath it. In *Lophiomus,* the illicium takes the form of a translucent fish larva—complete with a pair of beady black 'eyes' at the 'head' end.

Concealment of the Pupil?—The roundness and blackness of the pupil are concealed well enough when the iris as a whole is dark in color—though hiding the pupil in the iris only means that the whole iris is now as hard to hide as a pupil of the same size. In many fishes a thin black stripe, no wider than the pupil, may contain and absorb the latter. Such cases are enormously outnumbered, however, by those in which the pupil is rendered conspicuous or made to appear larger than it really is:

No more conspicuous pupils exist than those of most fishes, since the irides of most fishes are silvery. In birds, the iris may be dark brown (most passerines); but it may also be yellow, blue, green, etc. and these colors may contrast vividly with those of the feathers. Where the iris is brightly colored, the eye itself is rendered conspicuous and at the same time the pupil is rendered doubly so. This latter point may be dismissed as accidental; but not so the many instances among lizards, where not only is the range of iris colors greater than in birds, but even forms with

dark irides have these flecked with metallic pigments, making a quite gratuitous contrast with the black of the pupil. The common frogs, and many fishes and birds have the pupil outlined by a thin gold or silver line, the rest of the iris being so dark that the pupil would be beautifully concealed in it were it not for this metallic frame. To the adaptive colorationists, putting this ring around the pupil must seem about as mean a trick as hanging a bell on a cat.

In many diurnal snakes, particularly those of the racer type, a black blotch on the nasad part of the iris comes right to the edge of the pupil, which is otherwise bordered by a C-shaped metallic line. Thus the pupil appears egg-shaped, and nearly double its true area. If the gap in the C (which occurs just where the important forward-looking line of sight passes the pupil margin) exists to prevent distortion of the retinal image through diffraction at the border of the metallic pigment, then we have here an instance in which a very minor improvement in vision takes precedence over all considerations of iris-decoration for pupil-concealment.

One can only conclude that few animals have even apparently made any effort to conceal the pupil; and that great numbers, which could easily have made the pupil to blend with the iris, have 'spoiled it' by giving the pupil a false size, or a conspicuous outline, which serves no discernible purpose. Here, as with the eye as a whole, it is likely that the conspicuousness produced by glisten is so great that the animals have found it quite impossible to counteract the shininess by any sort of camouflage.

Sexual and Temporal Differences—Further indications of the general meaninglessness of eye colorations are seen in the species showing sexual dimorphism, and in those which have a capacity for changing the color of the iris from time to time. If eye colors are concealing, we should expect that if a few animals can change those colors, great numbers of others could and would do so. We might expect to find animals, even furred and feathered ones, blending their eyes into various backgrounds just as a flounder, by dermal color-changes, suits its whole body (*except* the eyes!) to the substrate. The chromatophores of the iris look enough like those which alter the skin pattern so that one wonders why they should not, as readily, alter the coloration of the iris.

Outside of the birds, there are but few animals which show a sexual difference in eye color. In the common adder of Europe, *Vipera berus,* the brown-and-black female has a light brown iris, while that of the gray-and-black male is red—a most unusual color for any iris to have, outside

of the fishes (where it is not uncommon, as for instance in the centrarchids). In our common box turtle (*Testudo carolina*) also, the male usually has a red iris and the female a yellowish or brownish one. These reptiles are such splendid examples of 'disruptive coloration'—as to their bodies—that they force one to believe not only that their eye colors are meaningless (in view of the colors themselves and the sexual difference) but that if they could have camouflaged their glistening eyes they would probably have done so.

There may even be great sexual differences in the apparent size, and hence conspicuousness, of the pupil—as in the boobies (see p. 226). Certain subspecific differences, like sexual ones, likewise suggest that eye colors mean little or nothing. For example, one subspecies (*kohnii*) of a certain terrapin (*Graptemys pseudogeographica*) has a most startling *snow-white* iris.

Most remarkable—and meaningless—of all differences are the temporal ones. The iris of a newborn human baby lacks stromal pigment and is consequently blue (p. 16)—even in a negro. Other primates show similar changes with age—the young *Indri,* for example, has greenish eyes while the adult has light brown ones. Deepening with age is particularly noticeable in the pigmentation of the iris of the domestic cat, which, like man, is always born with blue eyes. In some species of birds, the color of the iris changes markedly at different periods in the life cycle, while the changes in the plumage show no sort of correspondence. Charles Walker has noted that in young grackles the eyes are brown, becoming lighter with age—the reverse of what happens in cats and humans. In Brewer's blackbird (*Euphagus cyanocephalus*) the breeding male has a pale yellow iris, the breeding female a light brown one. In the rockhopper penguin, *Eudyptes cristatus,* the iris and the beak both vary from yellow to red and back again with the seasons. One change is as meaningless as the other, though both are doubtless expressions of the ebb and flow of sex hormones in the blood stream.

Even more rapid color-changes of the eye may occur, presumably mediated by dynamic changes in the iridocytes or perhaps by changes in the optical properties of the iris stroma, induced in turn by changes in the state of the iris muscles. Changes in the gross color of the iris have been reported to occur, in emotional states and in illness, in cats and in an occasional human. The eagle-owl of Europe, *Bubo bubo,* normally has the usual strigine lemon-yellow iris; but when the bird is angry, according to Arthur Thompson, the iris turns red and "seems to flash fire."

If the phenomenon is really as striking as all that, it may perhaps be legitimately classed as a 'warning display'.

Fishes, despite their extensive dermal changes, show little or no change in iris coloration with illumination. Trautman has noted, however, that in northern spotted bass (*Micropterus p. punctulatus*) dying of anoxia, all dark coloration fades from the iris, leaving it red and silvery. Ouradnik, while making color-photographs of narcotized rock bass, accidentally found that the eye would turn red in response to electric shock. Apparently noxious stimuli may contract the melanophores of fish irides, allowing other chromatophores to take charge of the coloration. But such phenomena cannot very well have any ecological significance.

Part III—Synoptic

Chapter 13

CYCLOSTOMES

(A) Lampreys

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Most lampreys live north of the equator, and these form the family Petromyzonidæ. In most of the genera of this family there are species which are parasitic as adults. From each of these large lampreys, one or more small, non-parasitic, 'brook' species has been derived. Some slight simplification of the eye (but no true degeneration) has occurred in all the brook lampreys, in keeping with the simplification of the whole body and the life-cycle.

South of the equator live two genera of parasitic forms, *Geotria* and *Mordacia,* which differ somewhat from each other and from the petromyzonid lampreys. Each perhaps deserves family rank; but their relationships are not yet sufficiently well known.

The Eye as a Whole—Of all non-degenerate vertebrate eyes, that of the lamprey is the simplest. The ocular patterns of any two of the other large groups of fishes will be found to differ from each other in only one or two major characteristics. The lamprey eye lacks all of these diagnostic features of higher fishes, and thus is primitive. But, it might as easily add one feature as another: the lamprey eye is disappointingly totipotential, and sheds no bright light upon the mode of origin of the peculiarities of any 'higher' eyes.

The lamprey orbit is not bounded, except in part, by the cranium, but by a spherical connective-tissue capsule. The extra-ocular muscles show some unique features, but none which could not—with a little revision—be brought into line with the situation in other vertebrates. They insert far forward, at the limbus, with some tendency to coalesce there. The inferior oblique and the internal rectus originate together, at a point farther nasally than the common point of origin (near the optic nerve) of the other three recti. The inferior oblique and the internal and superior recti are supplied by the third cranial (oculomotor) nerve, which in other vertebrates also innervates the inferior rectus (see Fig. 70, p. 172). In lampreys however the sixth (abducens) nerve not only supplies the external rectus as usual, but branches to the inferior rectus as well. This nerve emerges from the brain unusually far forward, and has been claimed to contain third-nerve fibers, which are perhaps those which go to the inferior rectus. The superior oblique is identifiable as such only by its nerve supply—from the fourth (trochlear) nerve—for it has a unique location, and inserts on the ventro-temporal quadrant of the eyeball. This has led some to refer to it as a 'posterior oblique', and to suggest that it is not homologous with the superior oblique of other vertebrate groups.

The corneal muscle (of accommodation), which is also outside the eyeball, is homologous with the oculomotor muscles inasmuch as it develops from one or two of the cephalic myotomes. It inserts into the skin of the spectacle which covers the cornea (Fig. 161).

The eyeball, as in all groups of fishes, is flattened anteriorly so that its antero-posterior axis is its shortest diameter. The major (equatorial) diameter varies from about 1.5mm. in the smallest brook forms (*e.g., Ichthyomyzon fossor, Eudontomyzon æpypterus*) to about 6.0mm. in the larger parasitic petromyzonids (*e.g., Entosphenus tridentatus*, landlocked *Petromyzon marinus*) and 7.0 mm. in *Geotria australis*.

The virtual space between the dermal spectacle and the cornea is occupied by a delicate mucoid tissue (thick in brook lampreys, thin in larger forms, where it may be almost lacking under the center of the spectacle), which belongs to neither structure, but is rather a continuation of the lining of the orbital capsule. The sclera is a thin membrane in brook lampreys. In the larger parasitic species it is relatively and absolutely thicker, and in the fundus may be as thick as the retina; but it is always purely fibrous in structure, never with any embedded cartilage or bone. Such a sclera may of course descend from an ancestral

cartilaginous one, as have those of the placental mammals and the snakes. Here in the lampreys however it may be regarded as primitive—particularly if one adheres to the dural theory of the evolutionary origin of the sclera (see p. 119), rather than to the older idea of a cartilaginous 'optic capsule' accompanying the hypothetical original chondrocranium. The cornea is very thin in all lampreys, consisting of little more than a Descemet's mesothelium and a thick Descemet's membrane. Since the cornea and the skin have not fused, there is of course no corneal epithelium—contributed in higher forms by the epidermis of the skin.

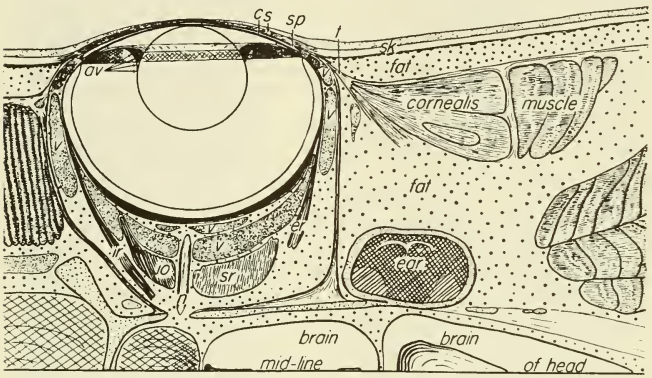

Fig. 161—The eye and surrounding structures in a lamprey, *Lampetra fluviatilis*, in horizontal section; the anterior end of the animal is to the left. Modified from Franz.

av- anterior surface of vitreous; *er*- external rectus; *io*- inferior oblique; *ir*- internal rectus; *n*- optic nerve; *s*- spectacle; *sk*- skin; *sp*- subspectacular space (virtual, and occupied by a mucoid continuation of the orbital capsule); *sr*- superior rectus; *t*- tendon of corneal muscle, inserted in spectacle; *v, v*- venous sinuses.

In the European river lamprey, *Lampetra fluviatilis*, the inner surface of the cornea, near the iris angle, bears a conspicuous thickening composed of epithelioid cells, much like the annular ligament of a teleost (see Fig. 169, p. 577). The cells may represent a piling-up of Descemet's mesothelium, though it has been claimed that the mesothelium passes over them and reflects onto the anterior face of the iris. The writer can see nothing of such an arrangement. No function has been suggested for the thickening. Delicate strands, perhaps coated with mesothelium, cross from it to the periphery of the iris, like a pectinate ligament. These

strands are present even in brook lampreys, in most of which the thickening is practically non-existent (except superiorly), and also in other parasitic lampreys—none of which has it so prominent as *Lampetra.*

The chorioid appears to differ markedly between parasitic lampreys and the various brook species in the same genera with them. In *Lampetra fluviatilis* and *Petromyzon marinus,* perhaps also in *Entosphenus tridentatus* (where an especially intense pigmentation interferes with observation), the outer half or more of the thick chorioid consists of a continuous lake of blood, the 'subscleral sinus'. This is presumably fed directly by the choriocapillaris, which in turn is supplied by small arteries in the more ordinary, inner, portion of the chorioid. The chorioid has no true veins; the arteries branch away from four main ones, one in each quadrant, which stem from a single artery which perforates the sclera just beneath the optic nerve. The chorioidal sinus is drained through the sclera by four apertures, called 'venæ vorticosæ' by courtesy, into a system of extra-ocular venous sinuses (Fig. 161, *v, v*) which fill the orbital capsule and cushion the eyeball, much as does the orbital fat of a higher vertebrate. These sinuses are present in brook lampreys also; but here, the chorioid is usually no thicker than the pigment epithelium of the retina, and indications of a subscleral sinus can be seen fairly clearly only in such large species as *Entosphenus lamottenii* (= *appendix*).

The iris has smooth inner and outer surfaces. The posterior layer of its retinal portion contains pigment only in the parasitic species, and then but little, mostly concentrated near the pupil. The anterior layer, which in other vertebrates gives rise to the sphincter and dilatator pupillæ, is epithelial and heavily pigmented in all lampreys. This situation is quite diagrammatically primitive, for the iridic continuations of the retinal pigment epithelium and the sensory retina thus preserve their respectively pigmented and unpigmented conditions in lampreys, instead of exchanging them (contrast Fig. 7g, p. 15). The lamprey iris possesses but little stroma, this in turn with little pigment or none. In brook forms, there is just enough stromal tissue to hold together the thin layer of blood vessels, which lies immediately against the retinal layers and forms apparently the anteriormost tissue of the thin iris. Large lampreys however have a substantially thick argentea layer anterior to the blood-vessel layer. It does not continue around the chorioid (*cf.* pp. 235-6). The blood-vessel layer in all lampreys is much like a choriocapillaris; but it is independently fed by three small, symmetrically-arranged arteries which enter the eyeball anteriorly.

The iris merges directly into the chorioid opposite the ora terminalis of the retina, without the intermediation of a ciliary body—since there are no ciliary muscles, ciliary processes, or zonule fibers, for which attachments need be supplied. The perfectly spherical lens is held against the

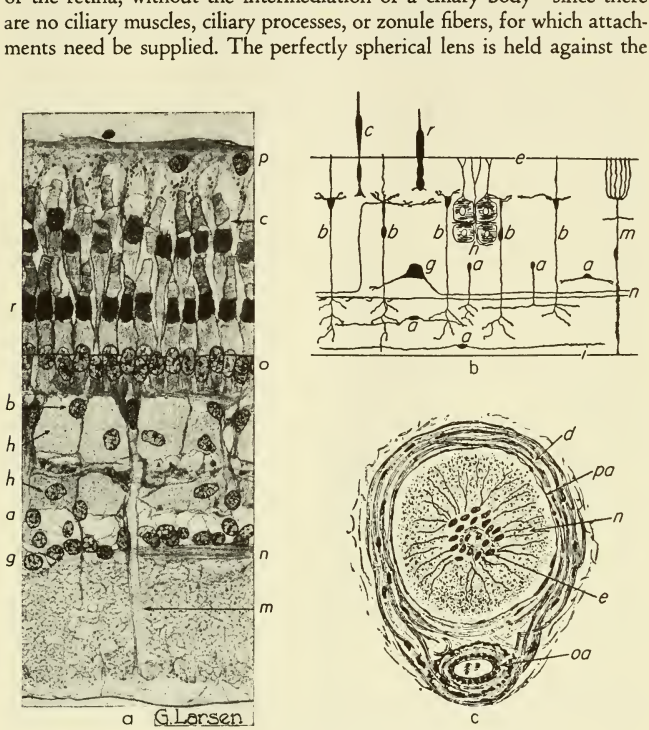

Fig. 162—Retina and optic nerve of *Lampetra fluviatilis*.

a, appearance in ordinary histological preparation. × 500.

a- amacrine cells; *b*- bipolar nucleus; *c*- cone; *g*- ganglion cells; *h, h*- horizontal cells; *m*- Müller fiber; *n*- nerve-fiber layer; *o*- outer nuclear layer; *p*- pigment epithelium; *r*- rods;

b, neurological schema, based upon Bielschowsky preparations. × 250. After Tretjakoff.

a, a- amacrine cells (six types); *b, b*- bipolar cells (five types); *c*- cone; *e*- external limiting membrane; *g*- ganglion cell; *h*- horizontal cells; *i*- internal limiting membrane; *m*- Müller fiber; *n*- nerve-fiber layer (= ganglion-cell axons); *r*- rod.

c, cross-section of optic nerve and its sheaths. From Franz, after Dücker.

d- dural sheath; *pa*- pia-arachnoid sheath; *n*- nerve-fiber mass; *e*- ependymal cell-bodies; *oa*- ophthalmic artery.

cornea by the vitreous. The surface ('hyaloid') membrane of the latter is conspicuous in microscopic sections, but it contains no blood vessels where it contacts the retina. Indeed, apart from the iris and chorioid there are no vascularized structures; and there is no canal of Schlemm.

The Retina—The lamprey retina (Fig. 162) differs from all others in that its ganglion cells are not separated from the inner nuclear layer. As a consequence, the nerve fiber layer lies embedded high in the retina instead of near its inner surface (*cf.* Fig. 19, p. 43). Though one cannot be certain, it is not likely that this is a primitive arrangement (nor does it smack of 'degeneracy'). True, in the histogenesis of any (other) retina the bodies of the ganglion cells are at first contiguous with those of the inner-nuclear elements; but it is stretching a point to suggest that this is an ontogenetic recapitulation of the adult cyclostome arrangement.

The lamprey optic nerve is, however, assuredly primitive in its organization. Running axially through it is a column of cell-bodies, appearing in cross-sections of the nerve as a rosette of nuclei, each of whose single processes radiates to the surface of the nerve. These cells are obviously ependymal—not of a higher, glial, type (which they have usually been called). If we think of the optic nerve as a cylinder, then its radius represents morphologically the thickness of the neural tube of which the retina is an evagination. The axis of the nerve—even though the nerve is not tubular, but solid—thus stands for the inner surface of the brain wall. Thus, each ependymal cell in the optic nerve maintains the orientation of any ependymal cell in a primitive brain (see pp. 126-9). Vertebrates above the lampreys all have at least neuroglial tissue, if not mesodermal connective tissue as well, forming the supporting framework of their optic nerves.

The visual cells of lampreys exhibit variations from genus to genus, but within the Petromyzonidæ these can be arranged in a fairly satisfactory series with regard to taxonomy. In the primitive genus *Ichthyomyzon* the rod and cone differ but little in length, and the outer segments of both are tapered, and to this extent, 'cone-like'. The rods outnumber the cones by five-to-one in the parasitic lake species *castaneus* and *unicuspis,* by three-to-two in the brook form *fossor.* In *Petromyzon* (Fig. 163b), the next higher genus in the scale, the cones have become much longer than the rods; and the rods, which here outnumber the cones three-to-one, have cylindrical outer segments of moderate length. This differentiation in length and shape reaches a maximum in *Entosphenus,* and the numerical predominance of the rods is greatest also in

E. tridentatus (8:1; in *lamottenii,* 1:1). *Lampetra fluviatilis* (Fig. 162), though a member of the culminant genus of the petromyzonid line, has its rod and cone outer segments of less unequal length, and even the rod outer segments are slightly tapered—thus, rod and cone are rather less well differentiated than those of *Entosphenus,* ranking just below *Lampetra.* The 1:1 ratio of rods to cones in *fluviatilis*—so close to the ratios in all brook lampreys, regardless of their taxonomic affinities—probably reflects the shallow-water habitat. The rods outnumber the cones most

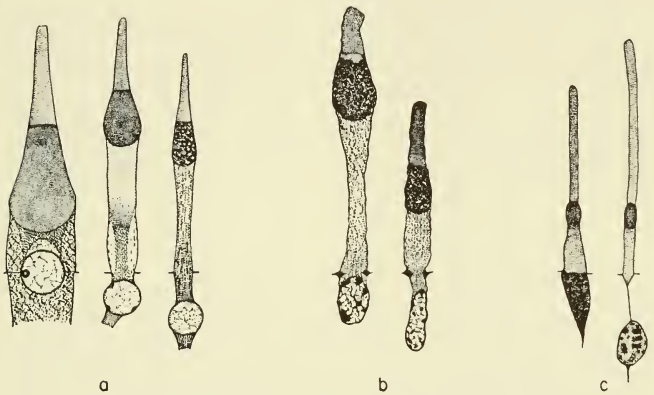

Fig. 163—Visual cells of lampreys and elasmobranchs. × 1000.

a, 'cone' types (at least one of them functionally a rod) of New Zealand lamprey, *Geotria australis.*

b, cone and rod of landlocked Atlantic lamprey, *Petromyzon marinus.*

c, cone and rod of smooth dogfish, *Mustelus canis* (redrawn from Schaper). In *M. mustelus* the cone is less rod-like in form, and in *Myliobatis aquila* it is fully differentiated; all other elasmobranchs have only rods, like that shown here.

greatly in the lake and marine lampreys, which, for their life in deeper waters, might be expected to require more rods for greater sensitivity to light.

On morphological grounds alone, it appears probable that the petromyzonid rod has evolved from a cone within the group, with *Ichthyomyzon* exhibiting an early stage in the process; and, from taxonomic considerations, it would seem that this rod must then have no connection with any other in the vertebrates (see Plate I). The visual cells of

Geotria (which genus some ichthyologists consider more primitive than, perhaps ancestral to, the petromyzonids) are all cone-like in form, and comprise three types in about equal numbers. The largest of these types may however contain rhodopsin as does the short (rod) cell in the petromyzonids—unlike the northern lampreys, *Geotria* is nocturnal, and should have at least one type of functional rod. In any event, the average petromyzonid pattern (Fig. 163b) shows neither an easy derivability from that of *Geotria* (Fig. 163a) nor any ready convertibility into the pattern of duplex selachians (Fig. 163c).

No well-preserved material of *Mordacia* has ever been described. As nearly as Franz could make out in his sections, most of the visual cells are identical and are rod-like in form, with interesting 'false oil-droplets'. The retina may truly be pure-rod, for the tiny pupil (0.2mm. in diameter in a 3.0mm. eyeball) suggests a sensitive retina. In that case, it was probably derived from an ancestral pure-cone one, something like that which *Geotria* APPEARS to have, by transmutation (see Plate I).

(B) Hags

In the hagfishes the eye may be nearly as large as that of a small species of brook lamprey; but it is quite degenerate, and these animals give no response to light. In *Eptatretus* and *Polistotrema* the eyeball, 1.0mm. (*E. dombey*) to 1.3mm. (*P. stouti*) in diameter, lies embedded at the skinward side of a mass of fat three times its size, which in turn is situated at a variable distance beneath the skin. There are no extra- or intra-ocular muscles, no nerves except a vestigial optic, and there is no pigment in either retina or uvea. There is no trace of a lens, though in the embryo a lens placode forms and then thins out as if discouraged. The sclera and chorioid are not differentiated from each other (*cf.* the normal embryology of these tissues—pp.114-6); and the adult retina, only half as thick (100μ) as the average vertebrate retina, is still actually an optic cup with a considerable remnant of the old optic-vesicle cavity (see Fig. 38, p. 106). In some individuals, the embryonic fissure persists.

The eye of *Myxine glutinosa* is even more completely degenerate (Fig. 133a, p. 387). The half-millimeter eyeball is practically filled by the retina, which is doubled so sharply upon itself that there is no room for a vitreous cavity.

Chapter 14

HIGHER FISHES

(A) Elasmobranchs

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Most families of sharks and rays are tropical or subtropical, with pelagic or benthic habits. The permanent residents of the temperate zones are mostly bottom-living forms. A few species of both sharks and rays live in fresh water. The chimæras are all deep-sea, bottom fishes. The ocular specializations of elasmobranchs are in the direction of dim-light activity, and most species are nocturnal.

The Eye as a Whole—Elasmobranch eyes are large relative to the body—largest of all (and with the largest lenses in proportion) in the chimæras and such deep-sea sharks as *Etmopterus,* relatively small in the partly-skyward-looking rays, smallest of all (except for an enormously overgrown scleral cartilage) in such blind deep-sea rays as *Benthobatis.*

Mobile upper and lower lids, sometimes also a nasoventral 'nictitans', are usually developed to a greater or lesser degree in sharks (Galeorhinidæ, especially), though without any obvious value to the animal (see Fig. 131b, p. 382). In forms whose nictitans is very active, the lower lid (of which the nictitans is really a continuation) is motionless. The nictitans alone is present, together with a circular, motionless lid-fold, in the hammerheads (genus *Sphyrna,* =*Zygæna*).

The oculomotor muscles of adults are orthodox, though in the embryo (in *Squalus,* at least) a mysterious extra muscle ('muscle E') appears and then degenerates. In *Chimæra,* which is primitive in many anatomical respects, the internal rectus originates far nasally as in lampreys; but in most elasmobranchs the four recti originate close together, and the orbit ordinarily affords room for them to form a cone as in mammals. They insert at about the equator of the eyeball, the internal rectus however a little behind and the external a bit ahead. The obliques originate close together, far forward, and share insertion-sites with the corresponding vertical recti. This arrangement—probably more primitive than that in living cyclostomes—is essentially preserved in higher fishes, and

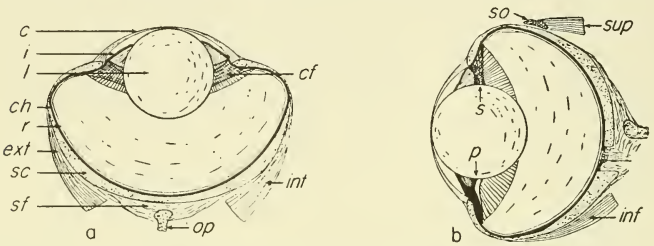

Fig. 164—The eye of a shark, *Carcharodon carcharius.* × 1⅓.
Combined from figures of Franz.

a, horizontal, b, vertical section. *c-* cornea; *cf-* ciliary folds, forming anchorage of gelatinous zonule; *ch-* choroid; *ext-* external rectus; *i-* iris; *inf-* inferior rectus; *int-* internal rectus; *l-* lens; *op-* optic pedicel; *p-* lens-muscle papilla (*cf.* Fig. 166); *r-* retina; *s-* suspensorium of lens; *sc-* scleral cartilage; *sf-* fibrous portion of sclera; *so-* superior oblique; *sup-* superior rectus.

indicates that the original function of the obliques was to impart compensatory reflex wheel-movements to the eyeball in the plane of its equator (Fig. 165; *cf.* Fig. 16, p. 37, and p. 303).

A characteristic structure of the orbit is the cartilaginous optic pedicel, running prop-like from cranium to eyeball. At the eyeball end, it is often expanded and cupped to fit a broad, low boss on the back of the sclera, thus forming a ball-and-socket joint for the rotation of the eyeball. In various genera it may be lacking (*Scylliorhinus,* deep-sea forms; always through disappearance?), or may not reach to the eyeball, or may even contact the eye but not the cranium (*Sphyrna*). In a few forms—sharks as well as rays—it is slender and so bent and elastic that its tendency to straighten itself can proptose the eyeball when the extra-ocular muscles

relax all together. This action, having the effect of a levator bulbi muscle, was perhaps its ancient, original function. Apart from the pedicel, the eyeball in various elasmobranchs is supported and cushioned in the orbit by masses of gelatinous connective tissue, lymph- or blood-sinuses (*cf.* lampreys), or combinations of these.

In sharks and chimæras the eyeball is regular in shape and usually is strongly ellipsoidal, with its longest diameter horizontal and its shortest

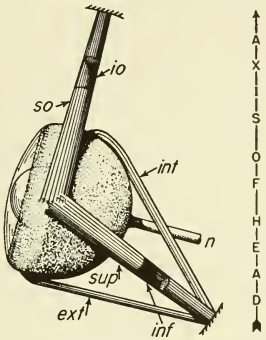

Fig. 165—Hypothetical primitive arrangement of the extra-ocular muscles in gnathostome fishes.

(The diagram shows the eyeball and the muscles as seen from the dorsal side, and emphasizes the favorable orientation of the obliques for the production of simple wheel movements of the eyeball in the plane of its equator).

ext- external rectus; *inf-* inferior rectus (revealed through gap in superior rectus); *int-* internal rectus; *io-* inferior oblique (revealed through gap in superior oblique); *n-* optic nerve; *so-* superior oblique; *sup-* superior rectus.

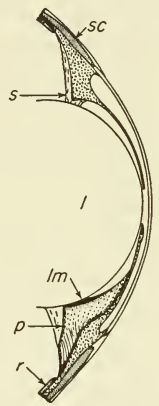

Fig. 166—Anterior segment of *Mustelus mustelus*. ×5. Combined from figures of Franz.

l- lens; *lm-* lens muscle (black); *p-* lens-muscle papilla; *r-* retina; *s-* suspensorium of lens; *sc-* scleral cartilage.

diameter the antero-posterior axis (Fig. 164). The eye is quite homogeneous structurally in these forms, with its greatest variations occurring in the sclera, which may be very thin as in chimæras and some deep-sea sharks (*e.g., Etmopterus*), or extremely thick as in the largest sharks. In one deep-sea shark, *Læmargus,* perhaps as a mark of degeneracy, the sclera sends massive cartilaginous diverticula into the chorioid. In most rays the depression of the body has involved the eyeball, producing a

distortion which may be best described as a flattening of the anterior dorsal region (Fig. 102b, p. 255).

The sclera is thickened not only fundally, to receive the optic pedicel, but also at the muscle-insertions and in a zone surrounding the cornea. It is usually thinnest at the equator. The sclera consists largely of a cup of hyaline cartilage, which is often calcified. The cornea is thick peripherally (and often opaque there, particularly dorsally and ventrally), thinner centrally, and is strongly arched in contrast to the flat corneæ of other kinds of fishes. The cornea is claimed to have all of the layers characteristic of the human, and even has a thick Bowman's membrane; but while a very thin, hard-looking cuticular membrane similar to a Descemet's membrane is present on the inner surface, the writer can make out no mesothelium whatever lying upon it (*Squalus acanthias*). The substantia propria is very neatly laminated, the fibers of each layer becoming progressively thinner toward the center of the cornea. Much of the thinning of the corneal center is accomplished by a dropping-out of layers, however. The epithelium may possess several times as many layers of cells as the human; but it is not cornified.

The chorioid is heavily pigmented, and typical in structure except for the inner one-fifth or so of its thickness, which in nearly all species is modified to form the remarkable tapetum lucidum characteristic of the group. Over a restricted area in the fundus, the chorioid is often markedly thickened by the presence, on its scleral side, of a so-called 'suprachorioidea'. This may consist of connective tissue with some blood-supply from large veins embedded in it, or it may consist largely of a tangle of such veins (possibly, then, a modification of the cyclostome subscleral sinus). The suprachorioidea is lacking in those species in which the optic pedicel is absent or is incomplete in extent, and the same reason seems to cover both lacks: less room than usual in the orbit, owing to a particularly large eyeball. To accommodate a suprachorioidea, the sclera is bowed outward, and the curvature of the retina is thus not disturbed. Between suprachorioidea and sclera there are believed to be lymph spaces, so that the chorioid and sclera are not conjoined firmly except near the limbus. Two arteries enter the eyeball, one temporally (which supplies the chorioid), the other ventrally (which runs forward through the chorioid to supply the iris); and two main veins, one dorsal, one ventral, leave it. Only the uvea is vascularized in the adult, though in embryos a vessel has been found to enter the embryonic fissure about midway of its length, thence sending branches forward and backward

along the retinal surface. This vessel is squeezed inexorably forward during development, however, as the embryonic fissure heals itself progressively forward from the fundus toward the periphery of the optic cup. The adult counterpart of this vessel may be the tiny one which supplies the lens-muscle papilla (*v. i.*).

The thin, broad, amuscular ciliary body bears low folds anteriorly, which may run up onto the back of the iris, and always leave a smooth orbicular zone behind them, toward the ora terminalis. The folds are meridional in sharks, but in rays are restricted to the dorsal and ventral quadrants (like the ciliary folds of the few teleosts that have them; and like the iris folds in many amphibians). A gelatinous zonule, shaped like a washer with a thickened rim, is anchored to the coronal region and to the lens near its equator. Further support is given the lens by a median dorsal, downward extension of the ciliary body into the zonule, forming a 'suspensory ligament'. Ventrally, the lens rests upon a cushion-like protuberance of the ciliary body. This papilla is in turn supported erect by a fin-like continuation of itself onto the back face of the iris. It is along the crest of this fin that the protractor lentis, the muscle of accommodation, is placed (Fig. 166). This little muscle is a derivative of (and indeed remains intercalated in) the pars ciliaris retinæ covering the papilla; hence, it is ectodermal. In its gross anatomical relationships, the lens-muscle papilla varies considerably from genus to genus of elasmobranchs; and as an extreme of this variation it may give a fair imitation of a teleostean falciform process together with its campanula (*q.v.*, pp. 582-3)—with which some of the elder anatomists seem to have confused it.

The iris is bowed forward in its middle by the subspherical lens, making the anterior chamber extremely shallow. Histologically, the iris is much like that of the parasitic lampreys, but with considerable pigmented stroma underlying the argentea (which, as in lampreys, is confined to the iris and does not embrace the chorioid). Some blood vessels are free in the stroma, but most lie against the retinal layers at the back of the iris. The posteriormost of the two retinal layers is devoid of pigment toward the root of the iris (as also in the ciliary body, as usual), but takes on more and more pigment toward the pupil until, for the pupillary one-third or so of the radial width of the iris, both retinal layers are heavily and about equally pigmented. The epithelio-muscular elements of the sphincter and dilatator (the former not so well separated from the parent epithelium as in man) are spindle-shaped, pigmented,

and autonomous and sluggish in their action. This musculature is scant in the deep-sea elasmobranchs, whose wide pupils are almost permanently open. At the root of the iris, the organ makes a slender angle with the cornea. There are no pectinate or annular ligaments in the iris-angle region, no loose meshwork tissue, and there is no canal of Schlemm.

The Retina—The elasmobranch retina is characteristically pure-rod, with a high ratio of visual to ganglion cells. This great summation helps to confer the photic sensitivity upon which the light-shunning habits of these fishes are based; but it necessitates a low visual acuity—estimated by Franz to be, on the average, 5% of that of man. Franz determined the number of fundal rods to be 10,800/sq. mm. in *Raja batis,* 21,600 in *Torpedo,* 24,000 - 75,000 in various small sharks, 100,000 in *Chimæra,* and 132,000 in *Etmopterus.* Corresponding ganglion-cell estimates were: *Raja batis,* 1500; *Torpedo,* 5000; the small sharks, 1200 - 3600; *Chimæra,* 600; and *Etmopterus,* 900.

The pigment epithelium is devoid of pigment (and usually, of cell-processes) over the whole extent of the sensory retina in all elasmobranchs except those few which lack the tapetum lucidum for obvious reasons: *Læmargus* (an abyssal shark), *Selache* (the basking shark), and *Myliobatis* (a pelagic ray with a cone-rich retina).

The horizontal cells in elasmobranchs are massive, much like those of lampreys (see Fig. 162a, b; p. 559). Though fine processes have been seen on them in Golgi preparations, it is unlikely that they have anything but a supporting function. The bipolar, amacrine, and ganglion cells are not confined to their 'proper' nuclear layers, but may occur out of position, in layers above or below. Such misplacements are quite characteristic of crude, scotopically-adapted retinæ in lower vertebrates.

Cones are known to occur only in one dogfish genus (*Mustelus*), the eagle ray *Myliobatis aquila,* and (doubtful!) the monk-fish, *Squatina.* They are least distinct from the rods, morphologically, in *Mustelus canis* (Fig. 163c, p. 561), better differentiated in *M. mustelus,* and are completely cone-like (*i.e.,* short, with plump inner segments and small outer ones) in *Myliobatis,* according to Mlle. Verrier. It seems clear that these few modern-elasmobranch cones are 'new', secondary derivatives of rods; but, the 'original' vertebrate cone must have persisted through the *ancient* elasmobranchs, in order to be handed on to the higher fishes—none of which, of course, were derived from sharks, rays, or chimæras (see Plate I).

The optic nerve has various cross-sectional shapes and septal patterns in the various species. In some, an axial core of ependymal or glial cell-bodies persists in the adult, reminiscent of the situation in the lampreys (p. 560; see Fig. 162c, p. 559).

(B) Chondrosteans

See also pages:
135-7 Fig. 60, taxonomy
150 photomechanical changes
160, 220-2 pupil
174 eye size and shape, optics
187 lack of area centralis
200-2 oil-droplets
235-6 argentea
238-42 Fig. 96, tapetum lucidum
264, 272-3 accommodation
292 binocular vision
381 streamlining
415-6 sclera
519-20 color vision

The living Chondrostei include the twenty-odd species of sturgeons (and shovel-nosed sturgeons) and the two genera of spoonbills, *Polyodon* and *Psephurus*. Most sturgeons are marine and anadromus; but a few (and the spoonbills) are confined to fresh water. All are bottom-feeders, with scotopically-adapted eyes. The eyes of the spoonbills have had practically no attention, and the ensuing statements apply solely to the sturgeons.

The Eye as a Whole—The firm margin of the orbit forms a broad horizontal ellipse, and is supported dorsally and ventrally, in the common European sturgeon (*Acipenser sturio*) and some others (but not *A. nasus*) by a pair of crescentic bones embedded in the conjunctiva. These have no phylogenetic connection with the scleral ossicles of either teleosts or sauropsidans. There are two venous sinuses in the orbit in most species, but the really important 'packing' around the eyeball consists of connective tissue. Concerning the extra-ocular muscles, no peculiarities are on record. The eyeball and cornea are slightly oblong horizontally, but not as much so as in most sharks.

The sclera is again cartilaginous, as in the elasmobranchs (and indeed all vertebrates excepting the cyclostomes, some teleosts and urodeles, the snakes, and the non-monotreme mammals). Obeying the 'rule' that where a relatively small eye lies in a large body its sclera is disproportionately thick (see p. 415), the scleral cartilage in the largest sturgeons is monstrously thickened in close imitation of the largest sharks (*Selache, Rhineodon*) and the whales (Fig. 167; *cf.* Fig. 141a, p. 413). It is of reasonable thickness, however, in such small-bodied, relatively large-eyed species as the American rock sturgeon, *A. fulvescens*. The

cornea is somewhat thinner centrally than peripherally, and is cloudy at its dorsal and ventral margins, as in elasmobranchs. In contrast to the latter, the sturgeons have a prominent Descemet's mesothelium, which is piled up at the iris angle to form an annular thickening from which a loose meshwork bridges over to the iris, isolating a large space comparable to that of Fontana in mammals (see pp. 679-80).

The chorioid is about as thick as the retina (and only a quarter as thick as the sclera), except for a small area in the fundus where a suprachorioidea of richly vascular character (as in some elasmobranchs) is superimposed upon it externally. To receive this, the sclera is locally

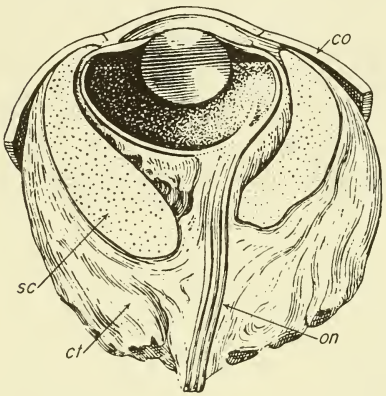

Fig. 167—Eye of a large sturgeon, *Acipenser sturio*. ×2½. From Franz, after Soemmerring. *co-* conjunctiva; *sc-* scleral cartilage; *ct-* connective tissue; *on-* optic nerve.

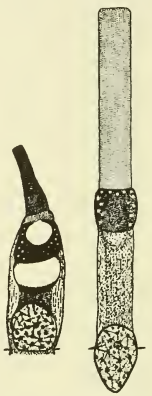

Fig. 168
Cone and rod from retina of a sturgeon, *Acipenser fulvescens*. ×1000.

thinned, not evaginated. The chorioid is silver-plated inside and out. The inner two-fifths of its thickness is occupied by the laminated, cellular, guanin-laden tapetum lucidum (Fig. 96, p. 242), which is separated from the retinal pigment epithelium only by the choriocapillaris, and extends forward even beyond the ora terminalis to dwindle away opposite the rim of the scleral cartilage. Externally, the chorioid is covered by a (thinner) layer of guaninized tissue—a true argentea, exactly comparable with that of *Amia* and the teleosts (and presumably directly ancestral thereto). It is *as if* either the tapetum or the argentea had been evolved first in the sturgeons, and the other of the two created by delamination, with

the unmodified chorioidal layers somehow getting in between them. In all probability, however, the sturgeons' argentea and tapetum were quite separate inventions despite their superficial histological resemblance. The argentea clings to the sclera even over the bump formed on the chorioid by the suprachorioidal cushion, and extends into the iris. Here it splits up into many lamellæ which occupy the whole thickness of the iris stroma and are sandwiched between layers of stromal connective tissue. The vascular supply of the eyeball, which relates solely to the uvea, has not been well worked out; but it apparently resembles somewhat the arrangement in elasmobranchs.

A 'ciliary body' can be recognized, with a little effort, between the ora terminalis and the portion of the uvea which is unmistakably freed from the fibrous tunic to form the iris; but its uveal portion is amuscular and differs in no important histological respects from the chorioid proper. In some European forms, this narrow zone is said to have meridional folds; but in *A. fulvescens* it is smooth. In all species, however, there is a mid-ventral papilla whose structure and homologies remain to be fully elucidated. Though it has been compared both with the elasmobranch lens-muscle papilla and with the teleostean campanula, it is not actually known to develop, embryologically, after the fashion of either. It apparently contains no muscle fibers, for Hess was unable to elicit any accommodatory changes in sturgeon eyes under electrical stimulation. The slightly flattened lens (Fig. 167) is suspended by a ligament quite like that in teleosts (see Fig. 105g, p. 261; Fig. 169, p. 577).

The iris is devoid of muscles, so that if we imagine the sturgeon eye to have evolved rather directly from one like that of a modern shark, we must say that it has reverted to the muscle-free condition of the lampreys—owing to the adoption of the bottom habit, with a renunciation of any shark-like tendency to bask (which would call for a mobile pupil to protect the sensitive retina developed for the benthic mode of life); and with a discard of accommodation, this being of no value to a scotopic eye with its crude resolution. In different quadrants* the pigmentation and the argenteal content of the iris stroma vary reciprocally, as if either reflection by the argentea or absorption in pigment were alone adequate to prevent light from getting through the tissue. But in regions where the iridic argentea is conspicuous, the distribution of

*Unfortunately the writer cannot be more specific, for the plane of section of his material (*A. fulvescens*, prepared by the late Harold D. Judd) is uncertain.

fuscin pigment in the retinal layers is as in elasmobranchs (p. 567); whereas, where there is much stromal pigment and little or no guanin, the posteriormost epithelial layer of the iris is quite unpigmented, as in lampreys.

The Retina—The sturgeon retina is characterized by a peculiar pigment epithelium, normal enough in its heavy pigmentation where it covers the 'ciliary body', but modified opposite the entire sensory retina in a manner best understood in connection with the discussion of the tapetum—pp. 238-9. Another peculiarity is the virtual absence of any distinct inner nuclear layer. The neuron cell-bodies which should form such a layer are displaced upward or downward by the great mass of horizontal cells (Fig. 96, p. 242); and the Müller fibers are not evenly distributed, but gathered into great bunches, their nuclei squeezed up to the lower surface of the outer nuclear layer. The outer nuclear layer is essentially single, but ragged, with the cone nuclei lying above the external limiting membrane, and the rod nuclei nearly always below it except in the periphery. Summation in the scanty ganglion cells is very great, and the overall threshold of stimulation of the retina should be very low, in keeping with the habits of these fishes.

The visual cells (Fig. 168, p. 570) are of two types—large rods, and single cones in smaller number. Here, for the first time (phylogenetically), we encounter cone oil-droplets in an extant vertebrate group. The oil-droplets are completely colorless in life (*A. fulvescens,* at least), but were assuredly not always so. The very fact that so many cones are present—though with their oil-droplets bleached in sympathy with a present avoidance of strong light—together with the presence of an apparently vestigial mechanism for moving the lens (the papilla described above, which suggests that the ancient chondrosteans did have accommodation), indicates that the primitive chondrosteans were diurnal, probably with smaller rods, more cones, and an accommodation equal to that of the teleosts. Moreover, though double cones (which are associated with bright-light vision) are lacking in living sturgeons, their presence (and identity of plan) in both the holosteans and the amphibians shows that the common ancestors of these groups, the primitive Chondrostei, must have had them (and presumably invented them; see Plate I). The oil-droplet is probably even more ancient, and indeed may have been present in the visual cells of vertebrates before these were *visual* in function: such pigmented oil-droplets are common in pigment-

epithelial cells (which are of course homologous with rods and cones); and similar vacuoles occur in some (*Ambystoma*) ependymal cells (see pp. 126-9 and Plate I).

(C) Holosteans and Teleosts

See also pages:
5 visual consciousness
44 Fig. 20e
52 optic chiasma
54 Fig. 22b
55 Fig. 23c
57-8, 60-1, 175-6, 216-7 visual cells
59 Fig. 24e
118 embryology
127 Fig. 55d
131 origin of lens muscle
134-5, 137 Fig. 60, taxonomy
145 habits
146-53 photomechanical changes
154, 157, 219-222, 228, 257 pupil
157, 231, 373-5 rhodopsin
158 Fig. 65
160-1 pupil, iris muscles, optics
164 energy economy
174 eye size and shape, optics
179 blind spot, optic nerve
184-5, 187, 190, 303-5 Fig. 77b, area and fovea
191, 193-6, 200-2 yellow cornea and its value
204, 405-7 eels
210, 212-3, 384-405 bottom, cave, parasitic, deep-sea fishes
230-241 eyeshine, tapetum
235-6 argentea
251, 254, 257, 260-3, 272-3 Fig. 98, accommodation
264-5 optics
268 value of vitreous
271, 380-1 Fig. 130, scleral ossicles
277 ciliary muscle
289-93, 320, 323-5, 331, 376-9 visual angles and fields
300-5 eye movements
349 movement-perception
362-5 stroboscopic vision
364, 466-7, 472-90, 518-9, 521-2 color vision
369-76 ocular adaptations to water
379-80 streamlining
381-4, 418 lids
414 comparison with whales
431-6 amphibious vision
450-4, 459-61 spectacles
524-37 dermal color changes
543-51 coloration of eye

The only living holosteans are the bowfin or freshwater dogfish (*Amia calva*) and the several species of gars (genus *Lepisosteus*). All are confined to North American fresh waters. *Amia* is restricted to the United States; *Lepisosteus* reaches south to Panama. Ancient holosteans were the ancestors of the teleosts, which are cosmopolitan and greatly outnumber all other kinds of fishes put together. The eyes of the handful of holosteans are best treated here together with those of the 20,000 species of teleosts; for, to all intents and purposes, the holostean eye *is* a teleost eye.

Holosteans—The extra-ocular muscles are normal in adults; certain of them run through canals in the bones of the skull. In *Amia* larvæ,

the internal rectus has a more anterior origin (primitive?—*cf.* lampreys, *Chimæra*), migrating backward during growth. The eyeball is somewhat ellipsoidal in *Lepisosteus* (*e.g.,* 19.5mm. horiz. x 17.5mm. vert. x 15.0 mm. axial), but is spherical in *Amia.*

The scleral cartilage is hyaline and thick, but is thinned fundally in *Amia* where it surrounds the 'chorioid gland' (*v.i.*). The cornea is likewise thick, as in large-eyed teleosts. The fibrous substantia propria is homogeneous; there is no canal of Schlemm. Descemet's mesothelium thickens at the iris angle to form a massive annular ligament, a cushion of epithelioid cells (said to contain glycogen) applied to the cornea. This thins abruptly to reflect onto the anterior surface of the iris, which thus has a mesothelial facing extending nearly to the pupil margin. *Amia* is the lowest vertebrate for which the presence of such a layer on the iris can be asserted with any assurance—and it is by no means certainly present in all forms above the holosteans.

The chorioid of *Amia* (but not of *Lepisosteus*) is modified by the presence of a chorioid gland. This structure, which is highly characteristic of the teleosts, is not a gland but rather is a great mass of capillaries, a three-dimensional *rete mirabile.* Its function is unknown, but it is probably not primarily nutritive. The best guess so far made is that it serves to smooth out the fluctuations of intra-ocular blood pressure which the heart-beat tends to produce, and thus insures a smooth flow of blood in the chorioidal vessels supplied from it, freeing the retina from mechanical disturbance. In *Amia,* as in teleosts, it is shaped like a bloated horseshoe, straddling the optic nerve with its opening directed ventrally. It is larger in *Amia* than in any known teleost, and is responsible for the spherical shape of the eyeball of *Amia*—whose actual intra-ocular cavity is flattened antero-posteriorly as in fishes generally.

There is an argentea, present only ventro-temporally in *Lepisosteus* but complete in *Amia,* where it splits into two layers to enclose the chorioid gland. The innermost of these layers comes almost close enough to the back of the retina to serve as a tapetum (like that in sturgeons) if it were wanted—but since most of the pigment in the chorioid is concentrated in a thin layer just outside the choriocapillaris, the inner argenteal layer is *hors de combat* as a reflecting device. Besides the chorioid gland, the argentea, and the usual vascular, pigmented connective tissue, the *Amia* chorioid contains many small venous sinuses.

There is a very narrow ciliary zone between the ora terminalis and the point where the uvea definitely bends away from the sclera to become

the iris stroma. The uvea here contains no ciliary or Brücke's muscle; but mid-ventrally there is a lens-muscle papilla or campanula. In *Amia* this is large, and the pigmented lens muscle blends with a definite tendon which in turn attaches to the lens capsule. In *Lepisosteus* the small muscle attaches directly without a tendon; but there is a meridional ridge (lacking in *Amia*) extending backward from the campanula about one-fourth of the way to the posterior pole of the eyeball, along the route of the old embryonic fissure. This ridge may be homologous with the teleostean falciform process (*v.i.*), but this is not certain; nor is it known for sure whether the holostean 'campanula' and lens muscle are even identical in function with the teleostean structures (*i.e.*, retractive, rather than protractive like the selachian lens muscle), let alone homologous therewith and ancestral thereto. The lens is supported from above by a squarish suspensory ligament (essentially a strap of tough vitreous—*cf.* sturgeons), with a broad insertion (4.0mm., in *Lepisosteus*) on the lens.

The iris is devoid of muscles. It bears meridional folds dorsally in *Lepisosteus* (as in rays and a few teleosts). Its anteriormost layer is the mesothelium (*v.s.*), following which comes a thin argentea continuing that of the chorioid, and a thick, pigmented stroma. The anteriormost retinal layer is heavily pigmented throughout, but the posteriormost is so only in the region where it is most exposed to light. Behind the annular ligament (which is semi-opaque) its pigmentation fades, so that there is a gradient from the pupil to the 'ciliary' region, where the innermost epithelial layer is completely bleached as in all vertebrates.

In both genera, the vitreo-retinal boundary consists of a delicate, presumably mesodermal membrane, in which is suspended a network of small blood vessels. These 'vitreal' or 'hyaloid'* vessels, first encountered here historically (but see p. 566, bottom), are common in teleosts and occur in some lungfishes and in amphibians, with imitations (of entirely separate origins) in snakes and mammals. They are clearly devoted to the nourishment of the inner layers of the retina, and will be discussed below in the paragraphs on the teleosts. In the holosteans, as in the amphibians and some teleosts (catfishes), the large artery and vein which supply the network enter the eyeball cavity at the mid-ventral point of the ora terminalis.

*No connection with the hyaloid vessels of the fetal mammalian eye—see p. 113.

The Holostean Retina—The retina of *Amia*—except for its visual-cell pattern—is quite in line with teleostean retinæ histologically. The lamina vitrea is particularly thick. The pigment-epithelial cells have long processes reaching nearly to the limitans. These are fine and multiple, so that the cell as a whole is structurally intermediate between those shown in Figure 20d and 20e (p. 44). The horizontal cells form two layers, those of the outer tending to be chunky parallelopipeds as in the lowest fishes, but the inner ones ropy and seemingly on the way to becoming fibrous and 'conductive' in appearance like those of the higher vertebrates (see p. 49). The bipolar and amacrine nuclei form the four loose remaining rows of the inner nuclear layer. The outer nuclear layer contains three ragged rows, the ganglion-cell layer a single scattered row of nuclei. The visual cells are described in connection with those of the teleosts (see Fig. 170b, p. 587).

The retina of *Lepisosteus* has never been fully described. Some vague statements of Mary McEwan suggest however that it is very much like that of *Amia*.

In both genera of holosteans the optic nerve is essentially circular in cross-sectional outline, but its nervous substance is in the form of a broad, thick ribbon which has been accordion-pleated edgewise to fit it into a tubular sheath. Correspondingly, the optic 'disc' or nerve head is not round, but vertically elongate as in many predaceous teleosts with similarly high cone-to-rod ratios (see pp. 179-80).

Teleosts—Ocular structure in the chondrostean-holostean-teleostean line culminates here in a pattern whose new features are of absorbing interest from the physiological and ecological standpoints, but must be studied purely for their own sake since they have not been passed on to any higher groups. We can make only physiological comparisons between the teleosts and the amphibians. The origins of all peculiarly amphibian ocular features must be sought far from these 'highest' fishes, in the imperfectly-known chondrostean-dipnoan-crossopterygian series of patterns.

The teleosts long ago split into two great lines: the malacopterygians (soft-rayed fishes), in most of which the swim-bladder, an ancient lung, remained open to the throat (hence the approximately equivalent name 'Physostomi' for these fishes); and the spiny-rayed fishes or acanthopterygians, all of which have the swim-bladder closed off, and belong to the 'Physoclisti' along with a few groups—synentognaths (halfbeaks, needlefishes), cyprinodonts (killifishes), and the 'Anacanthini' (cods,

grenadiers etc.)—which lack true spines (though the cyprinodonts, possibly also the anacanthines, are to be suspected of having once had them).

Figure 169 shows all of the principal morphological features which teleost eyes ever present, though of course not always with these particular sizes, shapes, and orientations. Each of these features may be present

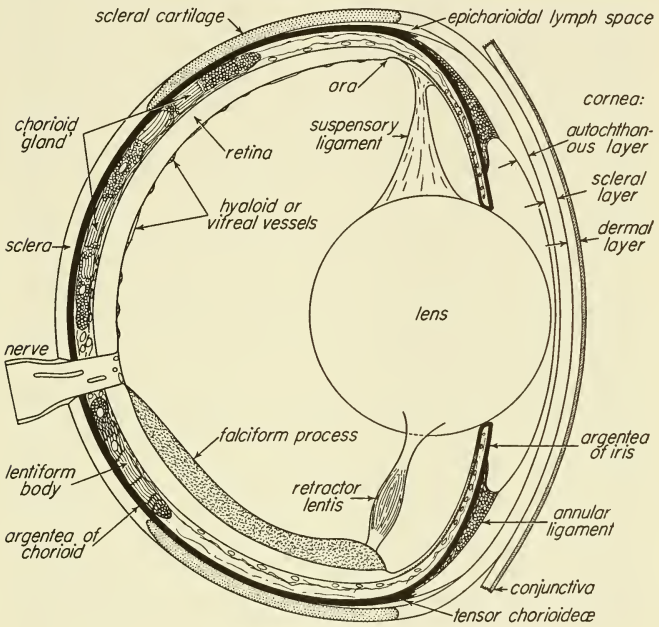

Fig. 169—Diagrammatic vertical section of typical teleost eye.

Certain of the structures may be lacking in a particular species (see text). A falciform process and a system of hyaloid vessels are never simultaneously present; and where the falciform process is lacking, the lentiform body is absent also. The argentea, shown in black, actually of course contains reflective, not absorptive, pigment.

or absent, usually independently of any others, from family to family or even within one family, without much regard to the families' taxonomic positions. Particularly, there is no feature which may not be present (or absent) in both malacopterygian and acanthopterygian

families. In other words, it appears that all of these special teleostean structures had been evolved before the great schism came; and, though in general the physostomes are anatomically a bit 'primitive' as compared with physoclists, there is no majestic progress to be seen in passing through the families of the one division to the families of the other.

The margin of the circumocular sulcus usually forms a narrow circular lid-fold, lapping onto the eyeball. Where the eye is retractile, temporary 'lids' may largely cover the eye (sometimes moved by a special dermal sphincter muscle, like an orbicularis); and 'adipose lids' (*q.v.*) are common in swift swimmers. The orbit is usually roomy unless the eyeball is very large or tubular. Cushioning venous sinuses are developed to greater or lesser degree, but other orbital structures are very variable and our knowledge of them lacks synthesis. A tenacular ligament often holds the eyeball in the orbit; this has no genetic relation to the selachian optic pedicel, for in some rays both structures are present side by side.

The oculomotor muscles are usually normal in number and arrangement (see Fig. 165, p. 565). They are often long, and are carried through canals in the bones of the skull—an anterior canal holding the two obliques, and a posterior one the four recti. There are no special retractor- or levator-bulbi muscles.

The eyeball is almost always flattened anteriorly, with its axial length its shortest diameter, and with its horizontal diameter tending to be its greatest dimension in swift forms, but more nearly equal to the vertical diameter in slow-swimming and small-eyed species. Since the corneal surface is eliminated optically, there is no need for it to be smooth; and it is often irregular, concentrically ridged, etc.

The sclera is very variable in its morphology. Primitively, it must have contained a complete cup of hyaline cartilage as in all lower fishes. It does contain at least some cartilage except in gymnotid eels, pearl-fishes, and a few others (where it is entirely tendinous) and in the tetras (where it is entirely bony). But in no instance is the cartilage-cup intact fundally —one might put it that the floor of the original cup, over the whole back of the eyeball, has been replaced by fibrous tissue. This fibrous window is often so large that the cartilage is restricted to a broad equatorial, or narrow just-post-limbal, ring (*e.g.*, pipefishes, many salmonids). The cartilage may also be widely distributed, not as one piece but in the form of little islands in a fibrous continuum (elephant-fishes). Typically there are thin plates of bone temporally and nasally, which may develop either anterior to the cartilage or external to it (the cartilage beneath them

then atrophying—*e.g.,* minnows)—occasionally, *from* preformed cartilage (*Salmo, Pagellus, Crenilabrus*). Both ossicles, only one, or none may occur within one family (herrings), and both are lacking in many small-eyed and bottom forms. Conversely, they may be enormous and joined to form a complete ring in large, large-eyed, swift swimmers (tuna, swordfish).

The cornea is also variable in make-up. Topographically, it is usually broad, and it tends to depart from a circular outline in the direction of a horizontally elliptical one, and to have its center shifted more or less nasally. These tendencies are more pronounced in swift swimmers than in slow ones, in marine forms than in freshwater species, and are obviously purposed to enlarge the binocular field with a minimal sacrifice of periscopy in the horizontal plane. Anatomically, the only constant feature of the teleost cornea is the portion of the substantia propria which is directly continuous with the cartilaginous and fibrous layers of the sclera, and which may be designated the 'scleral' portion of the cornea. External to this, and ordinarily fused with it, is an additional mass of tendinous substantia propria representing the dermis of the skin (see Fig. 151, p. 451), and bearing externally the (usually) thin corneal epithelium. This 'dermal' part of the cornea and the scleral layer are jointly homologous with the entire cornea in the chondrosteans and elasmobranchs; but, unlike those 'more primitive' fishes, teleosts have preserved a visible distinctness of the two layers, which moreover usually expresses itself in a ready separability of them. Although this situation would seem to be truly primitive—placing the teleost cornea between those of the lampreys and the elasmobranchs—interestingly enough it is particularly in some of the lower (physostome) teleosts that the substantia propria has become most nearly homogeneous and is no longer easily peeled apart into dermal and scleral laminæ (*e.g.,* salmonids, minnows, pikes).* The customary easy separability of the cornea has an evolutionary aspect as well as an immediate mechanical one, for it has led many times to the production of a 'spectacle' through a reversion to the primitive cyclostome situation in which the skin was not joined to the dural capsule of the eyeball.

*The homogeneity may be owing to the dermal propria's having actually disappeared from between the epithelium and the scleral propria. This appearance is given, for example, by the goldfish, where the dermal propria is either absent or consists at most of but a single layer of collagenous fibers continuous with such a layer in the conjunctiva. It may be that variations in the elaboration of the general head dermis can reflect in the laminations of the cornea.

A further major complication is introduced by the common or usual presence of an 'autochthonous' layer or mass of coarse-fibered substantia propria. This is distinct from and internal to the scleral layer, and always itself bears the thin Descemet's membrane and mesothelium (lacking in pikes?). Rarely, the scleral layer may be easily separable from the autochthonous, and may even (*e.g., Lepomis macrochirus*) bear inwardly a mesothelium for all the world like a Descemet's, though without any elastic, cuticular basement membrane. The phylogenetic origin of the autochthonous layer cannot be traced. It looks as if it had been formed *in situ* from 'nothing' (hence its name), magically interpolated between Descemet's membrane and the scleral propria. At the periphery of the cornea, the autochthonous layer usually thickens greatly, then abruptly tapers to a knife-edge termination opposite the front margin of the scleral cartilage or bone. Descemet's layers ordinarily do not extend nearly this far peripherally, for the mesothelium is reflected over (or forms) the annular ligament (see also p. 574) and continues back toward the pupil on the anterior face of the iris.

In a few fishes, including gobies and particularly the plectognaths (trunkfishes, puffers, ocean sunfishes etc.) the corneal substantia propria exhibits a complex lamination, with histologically peculiar intercalated layers which cannot be related at present to the typical lamination-system just described.

The 'annular ligament'—an inappropriate name, but one for which no good substitute has yet been offered—is almost universally present; but it can be greatly reduced or lacking in species of a genus which characteristically has it well developed (*e.g., Anabas*). It is no teleostean monopoly, but was invented by fishes as archaic as the Chondrostei, if not by the cyclostomes. The justification for calling it a ligament is the fact that it gives the appearance of forming a bracket between cornea and iris, holding them at a fixed angle to each other. Actually, the tissue of the ligament is (always?) so very ductile that it can have no such sustentative function. The ligament adds to the difficulty of defining the boundary between the iris and the ciliary body in teleosts, for one naturally tends to consider, as 'iris', only what is free of the annular ligament. Actually, the greater part of the iris—best defined as the portion of the uvea within the limbal circle—is covered by the ligament, and the true ciliary zone (from limbus to ora terminalis) is very narrow. Embryologically, the annular ligament arises from an accumulation of mesodermal cells which lie at the periphery of, and continuous with, the

Descemet's mesothelium of the cornea. Histologically, it is usually composed solidly of swollen or polyhedral epithelioid cells; but it may be loculated and vascularized (*Periophthalmus*) or dotted with melanophores and iridocytes (*Gadus*). In the bluegill, *Lepomis macrochirus,* the whole of the ligament appears to be occupied by a single lymph sinus (perhaps continuous with the epichorioidal one), which is crisscrossed by mesothelial trabeculæ. Where the tissue is solid and epithelioid, the cells contain granules which are perhaps always of glycogen, perhaps sometimes of other substances. The ligament then has a 'secretory' look; but what it may secrete, in the fashion of an endocrine gland, is a puzzle. It could conceivably be the source of either the whole of the aqueous humor, or of solutes which raise the osmotic pressure of the aqueous; but the ligament is no less well developed in freshwater teleosts than in marine ones. Occasionally, stuffed between the cornea and the annular ligament, or sometimes embedded in the latter (but never in the cornea or sclera), there is a 'canal of Schlemm', which has connections to iridic or hyaloid vessels and is obviously not homologous with the true Schlemm's canal of the sauropsidans and mammals.

The chorioid, in addition to the usual pigmented vascular layers, choriocapillaris, argentea (usually), and (occasionally) tapetum fibrosum, characteristically contains the same 'chorioid gland' which we noted in *Amia*—never as large, however, as there. It is ordinarily horseshoe-shaped, though it sometimes forms a complete ring around the optic nerve (some minnows), or may be divided in two parts as in one of the sea basses (*Labrax*). Between the limbs of the horseshoe, ventral to the optic nerve, there is a second body of the same histological sort—the 'lentiform body'—in some families and scattered genera.

The presence of the chorioid gland is rigidly dependent upon the presence of a 'pseudobranch', the vestigial hyoid gill which is found on the inner side of the operculum or gill-cover in most teleosts. The blood which has been aërated in the pseudobranch is gathered into an efferent artery which, in the neighborhood of the optic nerve, enters the sclera and breaks up into a set of capillaries in the chorioid gland. From these, the blood flows into the ordinary chorioidal circulation. In fishes which have lost the pseudobranch for any reason, the chorioid gland is inevitably lacking also. In general, this is true of small-eyed forms—catfishes, eels, characins, elephant-fishes, etc. In a similar way, the lentiform body is interpolated in the arterial supply to the falciform

process, and is lacking where the process itself is absent (as well as in many fishes which do have the process).

The falciform (*i.e.,* sickle-shaped) process is perhaps foreshadowed in holosteans (*Lepisosteus*), but it comes into prominence only in the teleosts. In its fullest development it is a ridge, formed of pigmented and vascular chorioidal tissue, which projects upward into the vitreous cavity from the floor of the eyeball. This protrusion of the chorioid through the retina is permitted by the fact that the lips of the embryonic fissure of the optic cup have never closed (see pp. 104-7). The falciform process consequently runs ventrally from the optic nerve head, and also veers nasally, tracing the course of the old embryonic fissure. Occasionally it appears to commence *above* the optic nerve; but this 'dorsal appendix' of the process is always unpigmented and lies on the retina, never projecting through it from behind.

There are great variations in the form and extent of the falciform process. It may be tall either proximally or (particularly, in physostomes) distally, or may be low throughout its length (most physoclists). In the needlefish, *Belone,* it is so tall and thin that it forms a partition in the whole ventral half of the eyeball, running from fundus to iris with contact on the lens over a full half-circle, and serving (through its elasticity) as the quick-acting antagonist of the muscle of accommodation in this agile fish. The process, if reduced in longitudinal extent, is always present distally (*i.e.,* toward the ora terminalis) and absent proximally (toward the fundus). Never does it commence at the optic disc and run only part-way to the ora; for any partial healing of the embryonic fissure in the sensory retina (tending to shorten the falciform process) always has a proximal→distal direction.* Instances in which the length of the process is thus somewhat reduced include the sticklebacks, wrasses, blennies, some cods, and some herrings. It is present only near the ora in minnows, pipefishes and sea-horses, clingfishes, the sprat, and the (American) pollack. Thus, there may be variations within a family (*e.g.,* Clupeidæ, Gadidæ).

Where the falciform process is wholly lacking (*e.g.,* elephant-fishes, eels, trunkfishes and puffers, anglers and batfishes), and in some instances where it is present but only far distally, there is a system of

*Since the definitive vitreous of vertebrates is always secreted by the sensory retina, it has a slit-like defect in teleosts—the 'vitreous cleft'—above the falciform process, which locally prevents such secretion (see Fig. 105a, *vc;* p. 261).

hyaloid vessels clinging to the inner surface of the retina (see also p. 575). These are usually supplied from the same artery which would otherwise go to the falciform process; but when the latter is absent the artery enters the vitreal cavity at the disc, and branches over the retina, instead of turning ventrally there to run through the chorioid along the line of the embryonic fissure. Falciform process and hyaloid vessels are thus mutually exclusive—a given teleost exhibits one or the other in full bloom, never both. Since the vitreal vessels are clearly concerned with the nutrition of the inner layers of the retina, it may be assumed that this is also the primary or sole function of the falciform process, from which nutrients (*e.g.*, glucose) could readily diffuse in all directions through the vitreous, to be absorbed therefrom by the retina. When in later chapters we compare the snakes with the lizards, and the mammals with the birds, we shall find in each case an exactly comparable situation: a mutual exclusiveness of two very different mechanisms for the nourishment of the nervous layers of the retina (see pp. 648-58).

At the distal end of the falciform process lies the 'campanula Halleri' or retractor lentis, with its ectodermal muscular elements and its pigmented investment derived respectively from the inner and outer layers of the blind retina. Occasionally very small or wholly lacking (*e.g.*, eels, gadids), the muscle when well developed still shows great variability with regard to size, shape, orientation, presence of tendons (derived from vitreous material) at one or both ends, etc. It pulls directly upon the subspherical lens (which is suspended pendulum-fashion from a dorsonasal suspensory-ligament thickening of vitreous), drawing it backward and temporad. This accommodatory apparatus, like the falciform process, may actually have been invented by the holosteans—possibly even by the chondrosteans (*q.v.*); but it is characteristically teleostean, and no semblance of it occurs in the land vertebrates or in the groups of fishes leading toward them (see next Section). The absence of the falciform process does not affect the presence of the campanula, though this, when a falciform process is present, is usually attached thereto; and the nerve and artery which supply the muscle emerge from the distal part of the process. The two structures sometimes coöperate particularly well, as in the mackerel (*Scomber scombrus*), where the falciform process lifts completely free of the retina and holds the campanula up to the lens.

The narrow ciliary zone of the uvea contains a few meridional muscle fibers, simulating closely the 'muscle of Brücke' which accomplishes accommodation in the Sauropsida and mammals. In teleosts, the ana-

tomical name which expresses its function (?) is 'tensor chorioideæ'. Though it is absent in those teleosts which have no accommodation, it is not directly concerned in that process—rather, it seems to serve to tauten the chorioid and retina around the vitreous body, thus preventing the backward-moving lens from using the vitreous to push the retina backward, which would defeat the accommodatory purpose of the retraction of the lens. This function of the muscle has never been established experimentally, however; and, strictly, its usefulness must be regarded as unknown.

In the ciliary zone, the chorioid merges imperceptibly into the true iris, which is fairly complex in structure. Typically, there is an anterior layer of mesothelium, continuous by way of the annular ligament with that of the cornea. Behind this is a thick argentea continuing that of the chorioid. The pigmented and very richly vascular stroma posterior to the argentea bears, superficially, a scattered layer of chromatophore cell-bodies whose processes perforate the argentea and expand within it, or more often anterior to it (beneath the mesothelium) to contribute to the externally-visible color pattern of the iris as a whole. The anteriormost of the epithelial retinal layers of the iris is always heavily pigmented except toward the pupil where it is converted into the lightly pigmented (sometimes unpigmented) 'sphincter'. The posterior retinal layer is pigmented only in the pupillary half of the iris, and is blank behind the annular ligament as in the ciliary zone. Between the stroma and the retinal layers there is a conspicuous membrane which gives one the impression of a myoid dilatator-sheet (as in the mammals—see Fig. 7b and g, p. 15); but this membrane is only a basement-membrane, comparable with the glass membrane in the region of the sensory retina—any dilatator elements ever present in teleosts are pigmented spindle-shaped cells, detached from the epithelium and lying in the stroma. The sphincter, when present, is not so well separated from the generative epithelium as it is in mammals. Very often a 'sphincter', sometimes a massive one, is present without demonstrable contractility. The vascularization of the iris is complex and variable, and its different plans in different groups have yet to be fully interpreted and unified; but the uncertainties here, in this blind-alley group of vertebrates, are of no consequence to the phylogenetic theme of these synoptic chapters.

The Teleost Retina—In so huge and diversified a class of vertebrates, the retina naturally shows great differences from one group to another. The fishes of the caves and crevices, muddy waters, and the deep sea

have been dealt with in the ecological chapters. Here, we can only generalize about the retinæ of the more ordinary teleosts, taking a little space to mention a few of the more outstanding departures from standard conditions.

The retina in teleosts varies more in thickness than in other vertebrate classes, from less than 100μ to more than 500μ. Much of this variation is caused by variation in the number of conductive elements per number of visual cells; but an unusual proportion of the thickness is usually occupied by the visual-cell + pigment-epithelial layers, owing to the need for scope for the extensive photomechanical changes characteristic of the group. The other layers exhibit a neatness and 'purity' (*i.e.,* an absence of ectopic elements) which we shall not see elsewhere until we reach the lizards, birds, and mammals. The horizontal cells usually have small bodies and slender (conductive?) processes, but occasionally—and not only in physostomes (*e.g., Esox*) but even in the 'highest' teleosts (*e.g., Stizostedion,* a percid) one encounters massive, stellate horizontals with broad bodies and short, thick, anastamosing processes—exactly like those of some of the lowest fishes. Where the cones are predominant, the piling up of conductive and integrative elements results in a thick inner nuclear layer and a compact ganglion-cell layer. At the other extreme is the situation in such a light-shunning fish as the bullhead, *Ameiurus nebulosus,* where the rods are large and the cones few and small (see Fig. 63, p. 147). Here, the outer nuclear layer contains only two rows of nuclei, the inner nuclear layer but one; the ganglion cells are widely scattered, and only 2/9 of the thickness of the whole retina lies between the external and internal limiting membranes.

The cells of the pigment epithelium are usually long, with most of the length contributed by their processes, which are few but thick, and reach nearly (or quite) to the external limiting membrane (Fig. 20e, p. 44). The migratory fuscin is usually in the form of needle-shaped granules, the stationary pigment in round granules. Guanin may also be present in large amounts, as in those minnows and perches which have evolved occlusible tapeta lucida, and also in many deep-sea fishes and in the Mormyridæ, Elopidæ, and Thunnidæ, some anchovies, some mackerels, the louvar, and one serranid (*Polyprion*).*

*These were not included in Table VII, pp. 240-1, as having effective tapeta, since the presence of pigment as well as guanin in some of them (together with the absence of any pronounced photomechanical changes) makes it questionable, without further study, how effective the guanin may be as a mirror.

In nearly all teleosts there are three types of visual cells: rods, single cones, and the twin cones which the teleosts monopolize (Fig. 170). In a particular retina, or in particular regions in some retinæ, only one of these, or any two of them, may occur. The pure-rod teleosts include the deep-sea forms and (according to Verrier) one siluroid, *Clarias batrachus*.* Twin cones alone occur in *Pollachius pollachius* and some *Gadus* spp.,† in *Scorpæna porcus, Sebastodes elongatus, Alosa finta,* and in all but the extreme periphery in a number of others—particularly flatfishes and swift surface forms (tunas, mackerels, mullets, etc.). The relative numbers of twin cones (where they are mingled with singles and with rods) decrease with an increase in the species' preferred depth of swimming. Clearly, the twin cone is associated with exposure to bright light.

The origin of the twin cone cannot be traced with certainty. It usually looks so much like two single cones fused together that this simplest explanation is the one dictated by the law of parsimony (see Plate I). But the holostean visual-cell assortment looks superficially much like the teleostean. Here (Fig. 170b) there are rods, single and *double* cones. The teleostean twin might have arisen from the holostean double through an equalization of the latter's two members, involving the loss of the accessory's paraboloid (the chief cone's oil-droplet being already long since gone in *Amia,* and replaced functionally there by a yellow cornea). Supporting this possibility is the fact that double cones, of sorts, do occur in teleosts—that is, conjugate elements whose two members are unlike in size and, to some extent, in structure. The oldest report of such elements is that of Greeff, who described them for *Rutilus rutilus* in 1900. The writer has found the conjugate elements of the goldfish (*Carassius auratus*) to be of this same sort. *Rutilus* and *Carassius* are both members of the minnow family (Cyprinidæ), which stands rather near the bottom of the malacopterygian division. The Salmonidæ rank about as low or lower; and Mlle. Verrier and Miss McEwan have described doubles, or unequal twins, for *Salmo gairdnerii irideus* and *S. trutta fario*. The occurrence of so many instances of unequal twins

*A dubious observation, for a few years later she reported rods and single cones, in equal numbers, for *Clarias dussumieri*.

†Tending to throw doubt upon the coryphænoidid ancestry of the cods (see pp. 389-9), since for the cods to have had pure-rod ancestors, and yet possess twin cones, would necessitate believing that they had invented twin cones for themselves. Still, the absence in gadids of accommodation and of scleral ossicles, together with the particularly easy 'splittability' of their corneæ, suggests that these fishes may well have risen secondarily from the ocean floor.

among the most primitive of living teleosts makes it seem fairly reasonable that the typical identical-twin cones of teleosts have indeed been derived from double elements like those of *Amia*. Against this view, however, must be placed the presence of double cones in *Fundulus* (see Fig. 24f, p. 59). *Fundulus* being one of the cyprinodonts, which (though they are soft-rayed physoclists) probably deserve a place near the perches at the top of the acanthopterygian heap, its double cones may well have been manufactured from ancestral typical twins. And if this has been

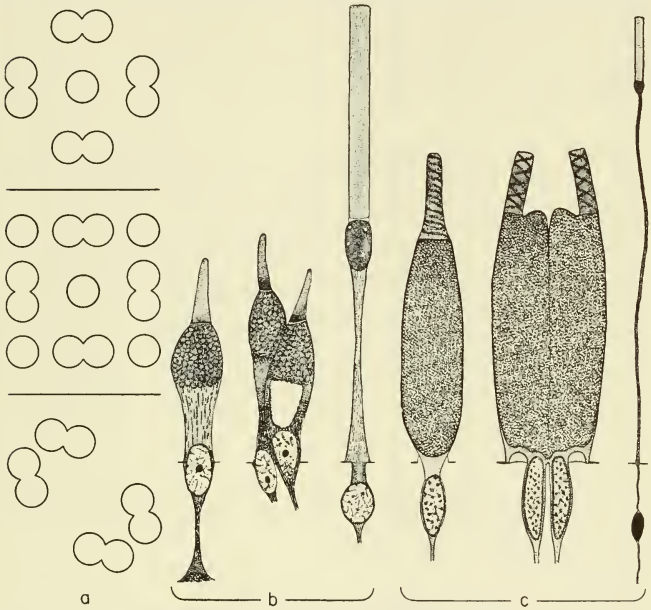

Fig. 170—Visual-cell patterns of holosteans and teleosts.

a, units of visual-cell mosaics in representative teleosts. Redrawn from Eigenmann and Schafer. Only the single and twin cones are shown—the (much smaller) rods fill the spaces around and among them; from above downward: commonest pattern, as seen in *Perca;* pattern in *Salmo* (without the central single, this would represent *Blennius*); pattern in *Scorpæna porcus*.

b, single cone, double cone, and rod of a holostean, *Amia calva*. ×1000.

c, single cone, twin cone, and rod of a teleost, *Stizostedion vitreum*. ×1000. Drawn from a preparation of George A. Moore.

possible once, it may have been possible many times, and secondary derivation from twins may thus account for *all* teleostean 'doubles'.

The visual cells are nearly always arranged in a neat mosaic; and where this is true, the unit of the mosaic is almost invariably a perfect square, with a twin cone on each side (Fig. 170a).* In some instances, where the visual cells are particularly large (*e.g.*, Fig. 170c), the mosaic is visible ophthalmoscopically in the living animal. Where the rods are very small and very numerous, as they usually are, they often occur in clusters or bouquets, with their myoids of unequal length so that the rod mass is pseudostratified—there being no room for the rods all to be brought into a single plane even in either extreme dark- or extreme light-adaptation. In two families—the elephant-fishes (Mormyridæ) and the ten-pounders (Elopidæ)—both rods and cones are gathered together into great bunches, each surrounded by the heavy conical processes of a circle of adjacent pigment-epithelial cells. In many teleosts, the cone nuclei lie partly or wholly through the external limiting membrane, and are much larger and less stainable than those of the rods (*cf.* Fig. 94, p. 237). The foot-pieces are then very different, those of the cones being heavy and dendritic while those of the rods are filamentous and terminate in tiny smooth end-knobs. These differentiations of nuclei and foot-pieces do not occur below the teleosts; nor do they appear on the land-animal side of the fence until the amniotes are reached. Though the physiological meaning of these differentiations is obscure, the sharing of them by the teleosts, birds, and placental mammals seems definitely correlated with the presence, in these same groups, of species having such things as extensive accommodation, high visual acuity, brief biological moments, foveæ, and color vision. The teleostean eye and retina, at their best, are outstanding in 'perfection' among all the fishes, and represent the fishes' nearest approach to the ocular quality of the very highest vertebrates.

(D) Cladistians and Dipnoans

These are the living 'lunged' fishes—though by no means the only ones which ever use the swim-bladder for breathing air at the surface. The two living cladistian genera, *Polypterus* and *Calamoichthys* (both inhabiting African rivers), were formerly classed as crossopterygians,

*Obviously, it would be decidedly worthwhile to make tangential sections of the retinæ of *Amia* and some of the Gadidæ; for if the conjugate elements of these forms are found to be arranged also in squares, our ideas about the origin of twin cones may be clarified.

but cannot now be considered at all close to the roots of the amphibian stock. The lungfishes strictly speaking (Dipnoi or Dipneusti), represented only by *Protopterus, Lepidosiren,* and *Neoceratodus* (living respectively in African, South American, and Australian rivers), are not too close to the amphibians either. The latter arose from the Crossopterygii, which were offshoots from an extinct dipnoan line. But unless and until the eye of the newly-discovered sole living crossopterygian fish, *Latimeria chalumnæ,* is sometime described, we have only the dipnoans to indicate to us how the amphibian eye may have evolved from its ultimate chondrostean ancestor (see Fig. 60, p. 135). The cladistians may be expected to be of some help also, for their connection with the chondrosteans is very close to the stem of the dipnoan-crossopterygian line.

Cladistians—Nothing is known concerning *Calamoichthys,* and the eye of *Polypterus* has had no more complete studies than the sketchy one of Leydig in 1854. The sclera exhibits the usual piscine hyaline-cartilage cup. In the chorioid there is a silvery layer, but it is unclear whether this is a guanin tapetum lucidum or an argentea (see p. 240). There are vitreal vessels, with their main vascular supply coming in at the midventral point of the ora as in *Amia* and amphibians (suggesting that the primitive chondrosteans may have had such vessels—see Fig. 60). There is no trace of any mechanism of accommodation. The retina is quite unknown; but the optic nerve has been described as having a number of branches, so that the optic papilla is multiple (see p. 367).

Dipnoans

See also pages:
135-6 Fig. 60, taxonomy, anatomy
150, 160, 220, 222-3 pupil
187 lack of area centralis
200, 216-7 visual cells, oil-droplets
263-4, 216-7 accommodation
525, 537 dermal color changes

Only the eye of *Protopterus* has been given any complete descriptions (by Hosch in 1904, Grynfeltt in 1911), and these have been faulty. All three genera are said to have nothing like a falciform process, and no accommodatory structures. There is of course no canal of Schlemm. *Lepidosiren* is claimed to lack the oblique muscles; little is known about its eyeball. The dearth of knowledge about *Lepidosiren* is of no great importance, since this form is in the same family as *Protopterus.* But *Neoceratodus* deserves a thorough investigation, for this large fish has none of the appearances of degeneracy characteristic of the Lepido-

sirenidæ. Its relatively large eye may have, in particular, a mechanism of accommodation; and its cone oil-droplets *may* be colored in life. But the animal is reputedly nocturnal (in captivity, at least), and may not have retained such things even though some diurnal ancestor may have had them. *Neoceratodus* (and *Latimeria*) remain our chief hope of ever learning the origin of the amphibian mechanism of accommodation, which is so distinct from those of all known fishes. Unless otherwise noted, the following statements apply only to *Protopterus* (*æthiopicus*):

The *ca.* 2.0mm. eyeball turns freely under a transparent dermal 'secondary spectacle' (*Lepidosiren* also). The cup-like scleral cartilage, which is about two cells thick, reaches only to the equator of the eyeball; but a fibrous continuation of it becomes, anteriorly, the inner portion of the cornea. The fibrous layer of the sclera external to the cartilage also continues forward as a portion of the corneal substantia propria, entirely unconnected with the skin of the spectacle (and apparently separate, or at least very readily separable, from the inner moiety of the cornea). The Descemet's membrane and mesothelium are the thinnest imaginable.

The chorioid consists of little more than a choriocapillaris, with only wisps of connective tissue, containing a very occasional pigment cell—altogether the thinnest, simplest chorioid outside of the blind vertebrates. There are no traces of a chorioid gland or of an argentea. The circulatory pattern of the eye includes a set of vitreal vessels (not in *Neoceratodus*—hence there, perhaps, a falciform process?).

The iris departs directly from the ora terminalis without the intercalation of any zone which could be called ciliary, and without support for its root in the form of any pectinate ligament or mass of meshwork tissue in the angle between it and the cornea. It is very thin—its stroma thinner than its retinal layers. Even the latter appear to have tried to thin out, for the pigmented anterior layer is squamous rather than cuboidal as usual. The posterior retinal layer is nearly free of pigment, so that the iris (and indeed, the whole eye) is as simple as that of a brook lamprey. The relatively huge (1.16mm.) lens lies entirely behind the iris, so that the pupil is free to change in size; and it can do so, in *Protopterus* at least, despite the total absence of any discernible modification of iridic cells into myoëpithelial elements.

The Dipnoan Retina—Here again, little can be said about *Neoceratodus,* and not much more about *Lepidosiren.* In the latter and in *Protopterus,* the pigment-epithelial cells are huge, the epithelium being as thick as the sclera and much thicker than the rudimented chorioid.

The processes are numerous, long, and filamentous (Fig. 20d, p. 44).

All of the retinal elements are monstrous, as are the cells in most of the organs of lepidosirenids. In *Protopterus* the outer nuclear layer contains two rows, each incomplete—more nuclei lie above the excessively delicate limitans than below it, and both rod and cone nuclei may occur in either location. The inner nuclear layer consists of four compact rows; and if horizontal cells are present, their cytosomes are as slenderly fibrous as those of the highest vertebrates. The outer plexiform layer is extremely thin, the inner plexiform thick as usual. There is a single row of ganglion cells. The optic nerve of *Protopterus* is a slender and simple cord, with an ependymal core as in lampreys; but in *Lepidosiren* and *Neoceratodus* the nerve fibers are blocked off by glial septa into fascicles, each with an axial core of (ependymal?) nuclei.

Protopterus has the most elaborate visual-cell pattern (Fig. 171 and Plate I). The rod exhibits a maximum of cone-like morphological features: it not only has the same cone-like (*i.e.*, particulate) nuclear chromatin as the rods of most lower vertebrates and the cones of all, but it also has a huge oil-droplet and a paraboloid (*cf.* Figs. 22, 23; pp. 54-5). This rod has certainly been secondarily derived from a cone, and the chances are that it is archaic, and represents the primitive chondrostean rod, changed but little or not at all. On the pathway leading toward the teleosts this rod promptly lost its oil-droplet (as did the cones at the holostean level, where the light-loving *Amia* has had to replace them with a yellow cornea); but here in the lungfishes the oil-droplet has persisted. There remains of course a possibility that the lungfish rod has been derived from a *lungfish* single cone.

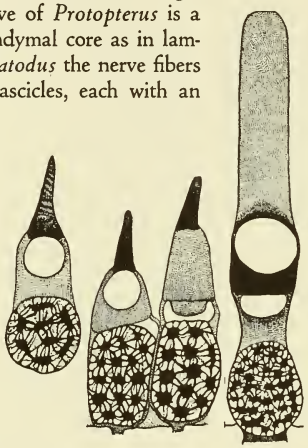

Fig. 171—Representative visual cells of African lungfish, *Protopterus æthiopicus*: single cone, double cone, and rod. ×1000.

In *Lepidosiren,* according to Kerr, there are only elements which seem identical with the rods of *Protopterus. Neoceratodus,* according to the half-century-old observations of Schiefferdecker, has only single cones with oil-droplets and rods without them.

Chapter 15

AMPHIBIANS

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In the fishes, the only important property of the cornea is its transparency to light (and, perhaps, to water). But when the vertebrates took over the dry land, the cornea at once presented advantages and disadvantages, which had to be dealt with. To remain transparent, succulent, and safe from injury, it had to be moistened by new glands and wiped and shielded by lids (see also pp. 418-9). In exchange for these attentions, the cornea offered the eye an opportunity to improve its methods of operation: the outer surface of the cornea, now exposed to air, became an important refractive surface. Some of the burden of focusing the image on the retina being thus taken off of the lens, the latter could now recede behind the iris. It then became easier to give the pupil extensive mobility; and, the lens being brought into the plane of the ciliary body, it became possible to discard lens-moving muscles and instead use the ciliary muscle for accommodation.

If the fishes had attempted to obtain these benefits, the withdrawal of the lens deep into the eyeball would have disastrously restricted the

visual field. But once the cornea and lens became able to embrace a wider cone of light-rays than the lens alone, there was no longer any need of having the lens placed as far forward in the eye as possible.

The Amphibia have never felt fully the penalties, nor completely realized the possibilities, in this situation. Their palpebral and glandular complexes have not had to be brought to the perfection demanded of the dry-skinned vertebrates; and they have clung to a lens-moving method of accommodation—indeed, one which they developed themselves—without having ever developed the ciliary body to such a degree that it could bear upon the lens and directly squeeze it.

The three living orders of amphibians are not closely inter-related. The origin of the cæcilians is quite unknown. The anurans and urodeles are usually held to have had separate origins from stegocephalians; but a modern theory, for which support is slowly growing, holds that the urodeles were derived directly from lungfishes. We shall find no ophthalmological reasons for considering the urodeles any closer to the lungfishes than the anurans; and we shall see that since the two groups share a number of new features—among them, such things as 'green' rods, retractor bulbi and protractor lentis muscles, discontinuous ciliary muscles, and fibrous zonules—there are good reasons for considering the tailed and tailless amphibians to have had common ancestry after all. Neither group can be called more primitive than the other; but the Anura are treated first here because their eyes are a little more complex, making it easy to describe the salamander eye largely by saying what anuran features it lacks.

(A) Anurans

According to Noble, the tailless amphibians comprise ten families in four suborders. The ocular structure of only two families—the Ranidæ (common frogs) in the highest suborder (Diplasiocœla), and the Bufonidæ (common toads) in the next highest (Procœla)—can be considered well worked out. Future researches on other families may alter some of the generalizations below.

The Eye as a Whole—At the time of metamorphosis from tadpole into adult, the lids and 'nictitans' develop; and the aquatic, benthonic tadpole's dermal spectacle then fuses with the primary dural cornea, except in the tongueless toads of the primitive family Pipidæ* and in one or

**Xenopus*, however, has a nictitans-like lower lid—though no upper.

two bufonids which are likewise permanently aquatic. The only massive gland present is the Harderian, which, like the other 'terrestrial' features (lids, nasolacrimal duct, flattening of lens, fusion of cornea and skin) develops during metamorphosis, and forms most of the packing for the eyeball in the largely membranous orbit. A broad and powerful retractor bulbi muscle—probably evolved by the bifurcation of the external rectus —is present, along with the six standard eye-muscles and a levator bulbi

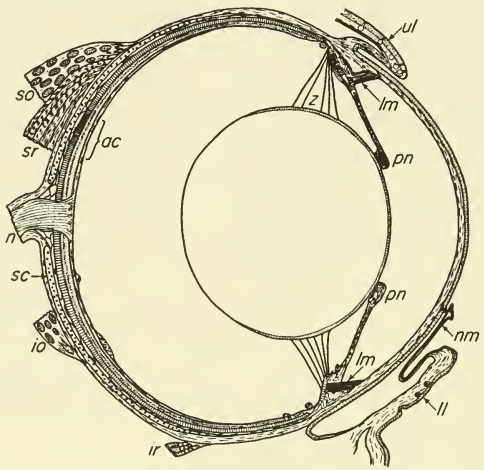

Fig. 172—The anuran eye in vertical section; semi-diagrammatic; based largely upon the leopard frog, *Rana pipiens*. ×11½.

ac- area centralis; *io-* inferior oblique; *ir-* inferior rectus; *ll-* lower lid; *lm, lm-* lens muscles (*cf.* Fig. 173); *n-* optic nerve; *nm-* 'nictitating membrane'; *pn, pn-* pupillary nodules; *sc-* scleral cartilage; *so-* superior oblique; *sr-* superior rectus; *ul-* upper lid; *z-* zonule.

stolen from the chewing-muscles. The retractor is of aid in swallowing food, as well as in the protection of the eyeball.

The eyeball is almost a perfect sphere, and has a deep anterior chamber owing to the arching of the cornea and the recessed position of the lens (Fig. 172). The curvature of the cornea blends smoothly into that of the sclera, but is sharpened at its apex. During or after metamorphosis, the fibrous sclera develops an extensive cup of hyaline cartilage, covered externally by connective tissue which reaches forward, beyond the rim of

the cup, to maintain continuity with the substantia propria of the cornea. The cartilage cup is usually thickest in the proximity of the optic nerve, and terminates anteriorly a little ahead of the rectus insertions. It is less extensive in this direction in *Bufo* than in *Rana, Pelobates,* and *Alytes.* It is soft and perforate in *Discoglossus,* discontinuous in some hylids (common tree-frogs), and lacking in at least one of them (*Pseudacris,* whose sclera is entirely fibrous, at least in the adult). In one microhylid, *Hypopachus incrassatus,* a bony ring replaces the cartilage anteriorly. The cornea is very broad, and has a *ca.* five-layered epithelium and a

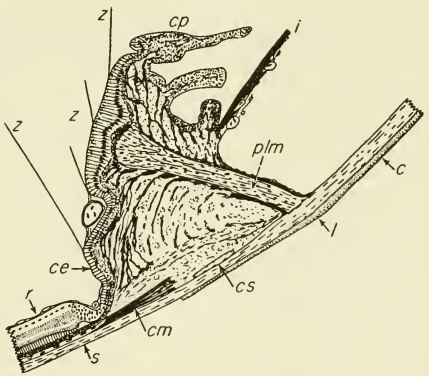

Fig. 173—The ventral ciliary process and associated structures in a frog, *Rana pipiens.* ×50. *c-* cornea; *ce-* ciliary epithelium; *cm-* ciliary muscle; *cp-* ciliary process; *cs-* canal of Schlemm; *i-* iris; *l-* limbus corneæ; *plm-* protractor lentis muscle; *r-* sensory retina; *s-* sclera; *z, z-* zonule fibers.

homogeneous substantia propria—both, thinner apically than peripherally. Both Descemet layers can be made out, though they are very thin.

The chorioid, apart from its choriocapillaris layer, consists largely of two pigmented membranes held apart by numerous broad, flat, pigmented struts, and enclosing between them a system of flat veins which tend to have parallel, vertical courses. The outer surface of the chorioid lacks an argentea, but may bear patches of xantholeucophores, guanin-filled iridocytes, etc., which show through the translucent sclera.

The ciliary body occupies a narrow zone and (in section) is essentially triangular, with the base of the triangle against the sclera just

behind the limbus. The posterior side of the triangle is faced with the usual two-layered ciliary epithelium, and distally bears nearly a hundred low folds, which continue meridionally onto the back of the iris. In *Rana,* these iris folds run nearly to the pupil; but in *Bufo* they go only half-way, and are lacking mid-dorsally and mid-ventrally (except for the two 'ciliary processes'). From the posterior, plicate face of the ciliary body, discrete cuticular fibers fan out to constitute a zonule; but these are embedded in vitreous, which fills what would otherwise be the posterior chamber. Mid-ventrally, a single prominent fold—large enough to be called a 'ciliary process'—runs from the ora terminalis to the pupil and there terminates in the ventral pupillary nodule (Fig. 172). Mid-dorsally, two or three large folds are approximated, and aligned with a dorsal pupillary nodule (possessed by most anurans in addition to the ventral one; exception: *Rana temporaria*). The zonule fibers stemming from these heaviest uveal folds are the most important for the suspension of the lens, and transmit the force which protracts it in the act of accommodation.

The anterior face of the ciliary triangle, bounding the anterior chamber peripherally, runs from the limbus (or, dorsally and ventrally, from the sclera behind the limbus) to the root of the iris, and is supposedly covered by a continuation of Descemet's mesothelium (which, however, if present at all, is in the form of a discontinuous patchwork). The central area of the triangle is filled by a meshwork of vascular and pigmented connective tissue, forming a pectinate ligament of a sort. At the base of the triangle, against the sclera, lie two structures which can best be seen in vertical sagittal sections of the eye: the ciliary muscle, and the canal of Schlemm. Neither of these forms a complete annulus around the anterior segment as in higher vertebrates, but both the muscle and the canal take the form of a dorsal-ventral pair of crescents, with gaps between their horns nasally and temporally. Each canal has connections with iris veins and, through the sclera, with conjunctival veins and arteries. Their comparability with the Schlemm's canals of higher vertebrates is most dubious; and even their function is in doubt, since they are often widely separated from the anterior chamber and the aqueous which they might be presumed to drain from the eyeball. Equally puzzling are the dorsal and ventral ciliary muscles. These contain meridional fibers, in some species circular ones as well. The meridional fibers run along the inner surface of the sclera to insert in the chorioid; but it is difficult to see, considering their location, what these muscles can accomplish. They

are credited in the literature with having been demonstrated, by electrical stimulation of the eye, to move the lens forward; but a little reading reveals that these experiments were made (by Beer) long years before the Russian anatomist Tretjakoff discovered the actual protractor lentis muscles. Since the accommodation of amphibians is 'positive', not 'negative' as in the teleosts, any use of the ciliary muscles as a 'tensor chorioideæ' (see p. 584) would seem only to interfere with accommodation. And yet, they *are* present in the sectors occupied by the accommodatory muscles:

The actual (or important) muscles of accommodation are two, a ventral and a dorsal (Figs. 172, 173, pp. 594, 595). They are of mesodermal origin embryologically, with no phylogenetic relationship to any muscles outside the Amphibia (though they are supplied by a branch of the oculomotor nerve, like the ectodermal teleostean retractor lentis). Each runs from the periphery of the cornea through the iris root (the ventral one passing through the old embryonic fissure) to insert within the ciliary 'triangle' near its posterior face, in the body of the median ciliary process. Their action is to draw forward these important anchorages of the zonule, and thus approximate the lens to the cornea. The large, firm lens is somewhat flattened, more so anteriorly than posteriorly. The ratio of its equatorial to its axial diameter is about 1.3:1—a direct optical consequence of the fact that the cornea, unlike that of a fish, is able (in air) to share in the production of the retinal image. This flattening is brought about ontogenetically just when it is needed; for the tadpole lens is spherical, and lies closer to the cornea as well, in close imitation of the optical situation in fishes.

In the iris, the stroma is thinner than the retinal layers—there is just enough of it to hold the blood vessels together; and some of the latter protrude through the anterior mesothelial 'layer' and bulge from the surface of the iris, almost free of it. The stroma contains iridosomes as well as melanophores, but there is no argentea layer. Both retinal layers are pigmented. The cells of the anteriormost are drawn out radially into spindles and constitute the dilatator pupillæ. This is lacking only in the region of the small, pigmented sphincter (beneath which the anterior layer is said to be continuous, as unmodified epithelium, to the pupil margin where it joins the squamous posterior retinal layer of the iris). Around the pupillary nodules, whose function is to lift the iris free of the lens to permit the surge of aqueous during accommodation, there are special arrangements of the retinal and uveal tissues. In some forms

with horizontal pupils (bufonids particularly), the nodules are large enough to meet when the pupil is fully contracted (see Fig. 87c, p. 223).

The circulation of the eyeball is complex, but because of the wide use of the frog in zoölogical teaching, we should perhaps consider it in some detail. As in 'ganoids' and in larval teleosts (before their pseudobranchs have differentiated), its main arterial supply is from a branch of the carotid, the 'ophthalmic artery', which on approaching the eye gives off two branches. These puncture the sclera above (or within) the vertically-ovoid disc, then diverge nasally and temporally in the chorioid to feed the choriocapillaris. The dorsal halves of both chorioid and ciliary body are drained by two veins which pass out through the sclera and unite as the superior bulbar vein. The ventral halves drain centripetally into a chorioidal venous 'star' from which an 'ophthalmic vein' leaves the sclera posteriorly to join the internal jugular.

The main trunk of the ophthalmic artery enters the sclera ventrotemporally and runs through the chorioid to the mid-ventral point of the ciliary body, where it gives off two branches and then turns backward onto the inner surface of the retina as the 'hyaloid artery'. The two aforementioned branches anastamose around the root of the iris to form a sort of major circle. From this, radial branches set up a plexus in the pupillary zone of the iris, which drains through radial veins (in the iris folds) into a venous rete in the ciliary body. This in turn is connected with the veins of the chorioid.

The hyaloid artery (*v.s.*) bifurcates nasally and temporally, these branches forming a nearly complete ring which lies just in front of the ora terminalis (Fig. 172, p. 594). Meridional vessels given off from this ring ramify backward over the retinal inner surface to generate a plexus of 'vitreal' vessels. These recombine into veins which assemble into nasal and temporal trunks (paralleling the arterial ring), and these in turn join with a mid-ventral trunk to form the 'hyaloid vein', which turns out through the chorioid alongside the hyaloid artery, and joins the ophthalmic vein (*v.s.*).

The Retina—The anuran retina is characterized by large, coarse elements reminiscent of those in *Protopterus* (see Fig. 64b, p. 148). It has the usual layers, and these have average thicknesses relative to each other. The horizontal cells have as fine fibers as the bipolars, and are apparently entirely conductive. The visual cells are thick in ranids, longer and more slender in bufonids and hylids in keeping with the nocturnality of the latter groups. They are of four types: single and

double cones, ordinary ('red') and 'green' rods (Figs. 64b, 174a). The foot-pieces of all four types are dendritic, and their nuclei also 'cone-like' (as to chromatin distribution). The red rods have their nuclei in contact with the external limiting membrane, a position usually reserved in other retinæ for the cone nuclei (since cones ordinarily have plump bases); the unusual plumpness of the amphibian red rod accounts for the location of its nucleus.

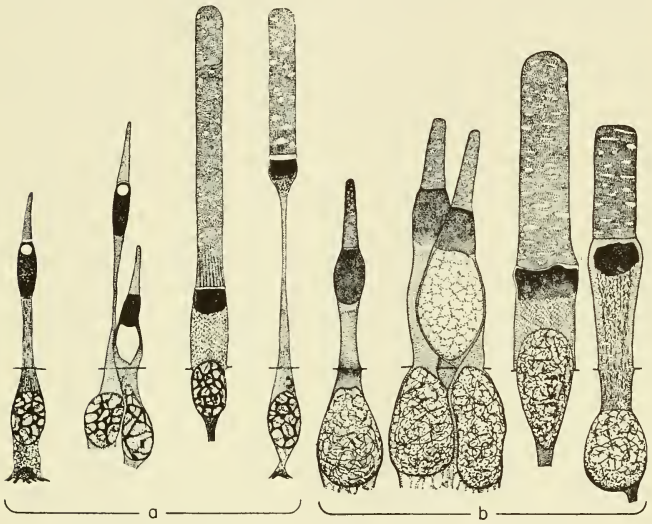

Fig. 174—Visual cells of anurans and urodeles. ×1000.

a, single cone, double cone, red rod, and green rod of leopard frog, *Rana pipiens* (in other families of anurans, the cones lack oil-droplets).

b, single cone, double cone, red rod, and green rod of tiger salamander, *Ambystoma tigrinum*.

The cones of ranid frogs possess oil-droplets, some at least of which are yellow in life; and the double elements are built on the standard plan (see Fig. 24a, b, c, p. 59). Bufonids and hylids, probably also other nocturnal forms (*e.g.*, pelobatids, brachycephalids,* microhylids, poly-

*Some of these however (*e.g.*, *Atelopus*, *Dendrobates*) are reported by the late G. K. Noble (personal communication) to be strongly diurnal. Such anurans may prove to have colored oil-droplets, or some substitute for them such as a yellow lens or cornea.

pedatids) differ from the arhythmic ranids in their total lack of oil-droplets.

The anuran (and urodele) visual-cell patterns share features in common with the holostean and with the dipnoan (see Fig. 170b, p. 587; Fig. 171, p. 591; and Plate I). The single and double cones of amphibians and those of *Amia* and of *Protopterus* are clearly homologous, respectively. It seems highly signficant however that the immature frog (tadpole) rod has been claimed by several investigators to have an oil-droplet, which it loses before or during metamorphosis. If this can be confirmed, the implication is that the frog's rods were once single cones. If their derivation was a recent one, then there may have been no rods at all in the stegocephalians (which, we may be sure, were diurnal—see pp. 164, 208, 274, 518-9). And, the cone-like characteristics of the amphibians' peculiar 'green' rod (see p. 58) make this element in a sense structurally, perhaps therefore genetically, intermediate between the single cone and the ordinary or red rod (Plate I). It is possible however that the Stegocephali did have a rod type, homologous with that of the Chondrostei and *Protopterus,* and that likewise it contained an oil-droplet—which the frog, in its infancy, still remembers. The presence of oil-droplets in the cones of both anuran amphibians and modern reptiles is proof enough that the common ancestors (Stegocephali) had such droplets—presumably, colored ones, else they would have gotten lost.

(B) Urodeles

The tailed amphibians compose eight families in five suborders. The members of four of these families (Crytobranchidæ, Amphiumidæ, Proteidæ, Sirenidæ) are 'larval' or 'partly metamorphosed' forms which are permanently aquatic, and whose eyes are in a state of degeneracy or on the ragged edge of it. Even among the other families—the primitive Hynobiidæ, their offshoots the Ambystomidæ and their cousins the Salamandridæ, and the latter's American derivatives the Plethodontidæ—there are scattered genera with greatly reduced or (cave-dwellers) wholly degenerate eyes. At its very best, as in newts and especially in terrestrial forms, the urodele eye is relatively small as compared with the anuran, and its importance to the animal is relatively less. It is also comparatively simple; but it cannot be too strongly emphasized that the urodele pattern is not to be looked upon either as directly ancestral to the anuran ocular plan, or as a descendant simplification thereof. The

resemblances between urodele and anuran eyes are by no means coincidental, but they represent only inheritances from a common ancestry of great antiquity—probably, a single stegocephalian type. Otherwise, some of the truly remarkable similarities would be hard to explain inasmuch as it is certain that neither the urodeles were ancestral to the anurans, nor *vice versa*.

The Eye as a Whole—Accompanying the usual oculorotatory muscles is a retractor bulbi which, as in anurans, may be contracted not only to protect the eyeball but also to use the latter as an aid to swallowing; for, the partition between orbit and mouth cavity is purely membranous. The lacrimal and Harderian glands are about equally prominent. Both are distributed along the lower lid, and are sometimes not discriminable. The lids form at metamorphosis if at all—they are lacking in the permanently aquatic forms; and there is never more than a rudimentary 'nictitans'.

The eyeball is spherical excepting in some of the good-eyed aquatic forms (*e.g., Onychodactylus,* some newts), in which the cornea is somewhat flattened in a fish-like manner. The cornea shows the same layers as that of *Rana,* and likewise is completed at metamorphosis in those salamanders which thereafter live on land. In the proteid *Necturus,* the primary cornea also fuses with the skin; but since no sulcus then forms around the eyeball, the latter is completely immobilized despite the presence of tiny extra-ocular muscles. This same situation perhaps obtains in some of the other half-transformed, permanently aquatic salamanders.

The lens being relatively enormous in keeping with the generally secretive habits of the group, the anterior chamber is shallow as compared with that of an anuran. The sclera contains the expected hyaline cartilage, but this is subject to great variations. In the Ambystomidæ it is a cup like that of the Anura, extending forward at least to the equator and persisting throughout life. But in their presumptive ancestors, the Hynobiidæ, the larval eye contains only a ring of cartilage (*cf.* teleosts), and this becomes fragmented at metamorphosis. In the salamandrids and plethodontids a larval ring disappears at metamorphosis, only bits of cartilage remaining in some individuals of certain species (*e.g., Triturus pyrrhogaster*). In the monstrous cryptobranchid *Megalobatrachus maximus,* on the other hand, the scleral cartilage is disharmoniously hypertrophied to a degree unmatched elsewhere in the vertebrates —in a horizontal section of the eyeball, two-thirds of its area is cartilage.

The cornea of this form is also abnormal in that it contains blood vessels (but the *ca.* 9mm. eyeball could not properly be called degenerate). The closely related *Cryptobranchus alleghaniensis* also has an overgrown scleral cartilage, equal in thickness to the radius of the lens. The connective-tissue capsule of the minute and vestigial eye of the only European cave salamander, *Proteus,* contains only bits of cartilage; and the cartilage in the sole American proteid, *Necturus,* is also discontinuous. Cartilage is sometimes present in the permanently larval American cave salamander *Typhlomolge,* but occurs in its relative, *Typhlotriton,* only prior to the metamorphosis which this cave salamander, alone of all such, experiences. In general, then, it may be said that whereas the anurans lack scleral cartilage as larvæ and possess it as adults, in the urodeles this situation is reversed. It would be interesting to know whether the tadpole of *Pseudacris* has scleral cartilage (see p. 595).

The chorioid is relatively thicker than in anurans, but more loosely organized, with pigmented connective-tissue membranes running in quite helter-skelter fashion. The circulation of the chorioid and iris is much as in *Rana,* but the details have not been as well worked out for any urodele. The ciliary body is triangular in meridional section and much smaller than in anurans. There are no folds on the ciliary body or the iris, excepting the single mid-ventral 'ciliary process' into which the accommodatory muscle inserts. The iridic portion of this process is essentially a seam formed by the closure of the embryonic fissure of the optic cup—such a seam is quite generally present in lower vertebrates, running all the way to the pupil margin.* Urodeles have no canal(s) of Schlemm; but crescentic ciliary muscles are present dorsally and ventrally in some forms (though not, apparently, in *Ambystoma*).

There are no pupillary nodules, but otherwise the structure of the iris is like that of the frog's. There is only a single, ventral, protractor lentis muscle. This appears to be strictly comparable with its anuran counterpart—and it will be recalled that an anuran can lack the dorsal muscle. The lens is relatively larger and more nearly spherical (especially in larvæ and aquatic adults) than in the Anura (*e.g., Necturus*—equatorial diameter only 1.05 × axial). It is most strongly supported by the mid-dorsal fibers of the anuran-like zonule (*cf.* fishes), less well by the mid-ventral ones, and depends least upon those in other sectors.

*It will be recalled that in mammals (see pp. 115-6) the blind part of the retina is not a portion, but rather an outgrowth, of the optic cup; hence, it never normally contains a portion of the embryonic fissure, which has healed before the commencement of the outgrowth.

The Retina—The retina of a salamander differs from that of a frog chiefly in the larger size and smaller number of its elements, and in the total absence of vitreal or hyaloid vessels. The latter are presumably dispensable owing to the smaller size of the eye and—probably—lower metabolic rate of the retina (owing to the paucity of cones). Large-eyed forms tend to have thin retinæ with extensive summation, the whole eye being thus devoted to sensitivity. Small-eyed forms have thicker retinæ, in which no great pains have been taken to promote sensitivity through summation or otherwise. But salamanders in general have much higher visual-to-ganglion cell ratios than do the frogs. Whereas *Rana pipiens* has about three visual cells per optic nerve fiber (within the area centralis), Burkhardt computed the following numbers of visual cells per opticus fiber in American salamanders: *Ambystoma maculatum,* 11; *A. jeffersonianum,* 8; *Triturus viridescens,* 7; *Eurycea bislineata,* 22; *Desmognathus fuscus,* 19; *Plethodon glutinosus,* 12; and *Hemidactylium scutatum,* 19.

The visual cells are of the same morphological types as those of anuran amphibians (Fig. 174, p. 599). Both rods and cones are present in all species excepting the four cave forms, whose visual cells are mere nubbins and all alike, reduced by degeneracy to a common denominator. But not all salamanders have green rods (they are definitely stated by European investigators to be lacking in *Salamandra,* though present in *Triton* [=*Triturus*]); and cones—particularly the double ones—may be sparse in strongly light-shunning forms (*e.g., Megalobatrachus*). Both the rods and the cones tend to be shorter and stouter than those of frogs and toads, and indeed the red rod of *Necturus,* two and a half times the diameter of that of a frog, is the thickest known to science.*

The absence of cone oil-droplets is in adaptation to the habits of the animals, as in non-ranid anurans, and does not prejudice against the presence of colored oil-droplets in the ancestral Stegocephali (see Plate I). In its own way, the urodele rod gives evidence of cone-ancestry: though it does not have an oil-droplet when immature (*cf. Rana*), it can and does sometimes exhibit another cone-organelle, the paraboloid (*e.g.,* in *Necturus*).

*It is for *Necturus* that the only counts of the retinal elements of an *entire* eye have ever been made for any vertebrate. Palmer, in 1922, found about 53,000 rods, 42,000 single cones, and 15,000 double cones in an average-sized retina, along with 176,000 inner-nuclear elements (26,734 of these being Müller fibers) and 30,464 ganglion-layer cell-bodies (most of them glial—the optic nerve, near the chiasma, showed only 962 fibers).

Comparison with Fishes—We should naturally like to find, in the eyes of the chondrostean→dipnoan→crossopterygian series of fishes, the prototypes of all the distinctively amphibian features. This is not possible; and we may never have the story much more complete, even if *Latimeria* is retaken and is studied by the right people. The eye of, say, *Ambystoma tigrinum* compares quite strikingly with that of *Protopterus;* but many of the similarities are matters of anatomy and of optics, and our attention here should be strictly on the morphology. Again, it is certain that the *Protopterus* eye has been secondarily simplified, and it is very likely indeed that the most complex of modern urodele eyes lack many features which the first urodeles possessed. Could we but restore the lost details to both *Protopterus* and *Ambystoma,* we might still find amazing similarity—or we might be unpleasantly surprised. When two structures, complex in two different ways, are simplified secondarily they may become closely identical without this having the least phylogenetic significance. Witness the similarity of the eye of *Protopterus* to that of a brook lamprey, no more closely related than an owl is to a gecko.

Such things as the amphibian tadpole's spectacle, and its spherical lens, are lungfish-like only because the tadpole is aquatic. The fact that the *Protopterus* lens lies behind the iris means only that the eye is disharmonious, not that it is pre-adapted for aërial vision. Some other parts of the *Protopterus* eye—the chorioid, for example—are too much reduced to afford any comparisons. Neither lungfishes nor amphibians have an annular ligament, which developed in the chondrosteans and went on up the holostean→teleost branch of the piscine tree; but this is a negative sort of resemblance—as well say that neither group has a chorioid gland; and, we have seen (brook lampreys!) that the structure can be absent in forms whose better-eyed relatives have it. Either ancient lungfishes, ancient amphibians, or both may have had annular ligaments as well as a number of other things.

Many amphibian features are entirely 'new', and while some of them may serve to link the group with higher forms, none can have any significance for the derivation of the amphibian ocular pattern from anything below. Among such features must certainly be listed the retractor and levator bulbi muscles, the extra-ocular glands, the lids, the iris folds (homoiologous, only, with those of elasmobranchs) and pupillary nodules of anurans, the loss of the argentea, the secondary absence of scleral cartilage in some adults and its delayed formation in urodeles, the protractor muscles (at least the dorsal one of anurans), the fibrous

zonule, the (secondary) absence of oil-droplets in most species, and the green rods of the retina. The 'canals of Schlemm' of anurans are probably unique, and the ciliary muscles are surely not the same thing as the teleostean 'tensor chorioideæ'.

But the amphibian eye is of course not wholly new. Though its iris muscles, like those of elasmobranchs (and teleosts), represent independent inventions, their beginnings are perhaps seen in the contractility of the unmodified iris epithelium of *Protopterus*. The mid-ventral 'ciliary process' may have been inherited ultimately from the similar structure in the chondrosteans, and may thus be a distant cousin of the campanula Halleri. A strong point is the identical course of blood supply to the vitreal vessels in anurans, *Protopterus*, and *Polypterus* (shared also with *Amia* and with the catfishes among the teleosts). The urodeles probably lack such vessels only through secondary loss. Most striking of all is the resemblance of the visual-cell patterns of *Protopterus* and the amphibians, emphasized diagrammatically in Plate I. When one considers however that the visual cells are phylogenetically the oldest and most fundamental elements in the whole eye, it should perhaps not be surprising that in the present instance they seem especially reliable illuminants of the dim pathway of phylogeny.

(C) Cæcilians

The Cæcilia or Gymnophiona are legless, worm-like amphibians which are restricted to the tropics. The single, homogeneous family contains 55 species in nineteen genera. All, except the aquatic *Typhlonectes*, spend most of their time underground. Their eyes are very small, but have well-developed retinæ and are useful for the registration of light-intensities and directions. The most important sense-organ is the unique retractile tentacle, which has both tactual and olfactory capacities. Several adjuncts of the eye have been commandeered by this more useful organ. The eyes of the Ceylonese *Ichthyophis glutinosus* and of *Hypogeophis alternans*, a resident of the Seychelles, have been the most completely investigated.

The orbit is capacious, but is largely filled by the Harderian gland, here serving to lubricate the sensory tentacle instead of the eye.* The eyeball is two-thirds of a millimeter in diameter in a large *Ichthyophis*,

*This is not the only instance in which the Harderian has ceased to serve the eye primarily, and has taken on a new function (see pp. 424, 455, and 635).

only 0.3mm. in *Hypogeophis*. The rotatory muscles are present in both genera (lacking in *Cæcilia* and *Herpele*), though thin and largely tendinous, and incapable of moving the eye owing to its attachment to the overlying skin. In the larva, a retractor bulbi is properly attached to the globe, but in later development it is seduced away by the tentacle to become *its* retractor. The internal rectus serves to retract the tentacle sheath, and a former levator bulbi is pressed into service as a compressor muscle of the tentacular (Harderian) gland.

The eyeball lies beneath a transparent patch of skin, from which it is separate only in the larva. In *Hypogeophis*, the primary cornea, a continuation of the fibrous sclera, can still be identified after fusion with the skin in the adult; but in the adult *Ichthyophis* the sclera appears to intersect the corium of the skin, and the lens to contact the latter directly. The chorioid is very thin, and is pigmented in *Ichthyophis* but not in *Hypogeophis*. There is no ciliary body or any mechanism of accommodation, and the iris consists entirely of the two epithelial retinal layers, only the anterior of which is pigmented. The pupil is the same size as the lens, which projects half-way through the aperture. The relatively large lens is solid, somewhat flattened, and is cloudy in life (in *Hypogeophis*, at least). Running through the small vitreous cavity from retina to lens, in the position of a canal of Cloquet, is a strand of (mesodermal?) tissue.

The retina is quite respectable. There are no vitreal vessels. The pigment epithelium bears many fine, pigmented processes, in which there is no pigment migration. Only massive rods, simple in structure (no oil-droplets or paraboloids) are present. In *Hypogeophis* the outer nuclear layer has two to three rows of nuclei, the inner nuclear three, and the ganglion layer two. Corresponding figures for *Ichthyophis* are: 2, 2-3, 1. In the latter genus the optic papilla is triple, the three branches of the optic nerve lying in one vertical plane (*cf. Polypterus*). No optic chiasma is visible outside the brain.

Chapter 16

REPTILES

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58-9 visual cells
118-9 embryology
134-9 origin, relationships
150 photomechanical changes
164-5, 205, 208 habits
187, 306-7 area centralis, fovea
210 fossorial forms
240-1 tapeta, eyeshine
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257, 269-83, 417 accommodation, refraction
293-6 visual fields
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339 Fig. 124c, parietal eye
365 pecten (conus)
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494-7, 518-20 color vision
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The eyes of the various types of reptiles are much alike except for the snakes, which are set sharply off from all the others. The class as a whole exhibits a number of features whose origins cannot be traced by any scrutiny of living amphibians. If a good fairy should offer the comparative ophthalmologist a living specimen of any one archaic vertebrate, his choice should certainly be *Seymouria,* that stegocephalian which was the 'first reptile'. Lacking such a miraculous resurrection, we are no better able to link the exclusive features of the reptilian ocular pattern to the elements of the amphibian plan, than we were to see the origins of the lissamphibian features in any of the so-far-studied lunged fishes.

The reptiles perfected the terrestrially-adaptive accessory organs which the amphibians had been forced to invent, and also made the most of their opportunity to develop a powerful, lens-squeezing mechanism of accommodation (see pp. 417-23, 592-3). Their most characteristic intraocular features are all means to this latter end: the striated ciliary muscle fixed (usually) to the rim of the cornea, the scleral ossicles and the concavity which they support, the 'ringwulst' or annular pad of the lens, and the tall ciliary processes which are fused to the lens capsule and are in all probability genetically independent of the uveal folds of modern tailless amphibians. Along with these structures, the reptiles have produced a striated (though ectodermal) iris musculature and a pigmented, richly vascularized, conical protrusion from the optic nerve head (the 'conus papillaris'), whose framework is ectodermal (neuroglial) and whose function is to nourish the inner layers of the retina (in lieu of vitreal or intrinsic retinal vessels) by diffusion through the vitreous, after

the fashion of the teleostean falciform process. Of all the reptilian peculiarities, only the transversalis muscle may be homologous with anything in the living amphibians (*i.e.*, with their ventral protractor lentis). The early reptiles adopted strict diurnality and a pure-cone retina; but many of the living forms and sub-groups have backslid into nocturnality, supporting this habit with a rod-rich or even pure-rod retina whose rods are transmuted cones in every case.

To every one of the above statements the snakes constitute a conspicuous exception. There is nothing whatever 'reptilian' about their eyes, which exhibit instead a number of features which are uniquely ophidian. Indeed, the snake eye is such a conglomeration of 'Ersatz' that it might well be imagined to have come from another world. Zoölogists have long been fond of citing the cephalopod molluscs, as showing how nearly an invertebrate group can imitate the vertebrate eye if it tries hard (see Fig. 1g, p. 3). They might give at least as much credit to the snakes; for in them, we see a *vertebrate* group which has been under the necessity of duplicating the vertebrate eye, and has made a very good job of it. This no doubt obscure statement will be clarified by the discussion in Section D.

(A) Chelonians

See also pages:
59 Fig. 24c
72 vision
101-2 zapfensubstanz
135, 138 Fig. 60, relationships
177 retina
184, 187, 190, 305 area centralis, fovea
186 Fig. 78
191-8, 202 oil-droplets
216 visual cells
224 pupil
251 Fig. 100
272-9, 436-8 accommodation, refraction
274 scleral ossicles
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340 parietal eye
344 movement-perception
422-3, 428, 450, 457-8 adnexa
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494-6, 519 color vision
546-7 coloration of eye

Though obviously highly specialized, the Chelonia are nevertheless the most archaic of the living orders of reptiles—closest of all to the stem group, the Cotylosauria. They are cosmopolitan, and comprise eleven families in four suborders. The taxonomic differentiation of the group is of less importance to us here than the ecological—into the strictly aquatic marine 'turtles' (*s.s.*), the amphibious, freshwater 'terrapins', and the strictly terrestrial 'tortoises' (see, especially, the references to accommodation and adnexa).

The Eye as a Whole—The eyeball has equal vertical and horizontal diameters, and a slightly shorter axial diameter (Fig. 175). Its internal proportions are those of a diurnal eye with a broad retinal image and high resolution. At the same time, its dioptric media are the most transparent known—which one would expect to be true of some *nocturnal* animal.

The sclera consists largely of a cup of cartilage which reaches forward beyond the equator, from where the zone occupied by the scleral ossicles extends to the corneal rim as a flat-surfaced, truncated cone. The cornea is thick (except in sea turtles?) and bears a relatively thick epithelium and prominent Descemet's layers. The substantia propria, at the limbus, divides into two portions, the inner of which receives the tendinous

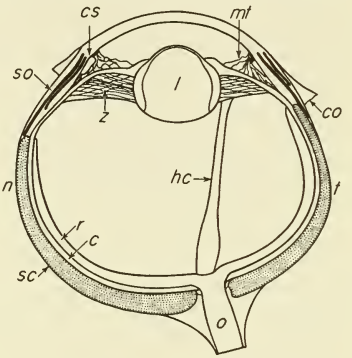

Fig. 175—Right eye of a turtle, *Testudo græca,* in horizontal section. Redrawn, modified, from Szent-Györgyi. (The lens is shown in full accommodation).

c- chorioid; *co-* conjunctiva; *cs-* canal of Schlemm; *hc-* hyaloid canal of vitreous; *l-* lens; *mt-* meshwork tissue of iris angle; *n-* nasal side; *o-* optic nerve; *r-* retina; *sc-* scleral cartilage; *so-* scleral ossicles; *t-* temporal side; *z-* zonule.

origins of the ciliary-muscle fibers, while the outer splits to enclose the scleral ossicles and then recombines to pass over the outer surface of the scleral cartilage as the fibrous layer of the sclera. As in reptiles in general, the boundary between cornea and sclera is indicated by a deposit of pigment in the fibrous tunic.

The chorioid is of ordinary thickness and is not richly vascular except in marine forms. Anteriorly, where the chorioid merges into the ciliary body, the inner layers of the uveal coat, together with their epithelial (retinal) facing, swing gradually away from the fibrous tunic, leaving a long, sharp cleft to be filled in with loose connective tissue which thus suspends the iris from the limbus corneæ. The canal of Schlemm lies against the sclera in this meshwork tissue, in a position approximating

closely that of the amphibian canals (see Fig. 173, p. 595). This early divergence (*i.e.*, as one passes forward from behind) of the uvea and sclera—characteristic also of other reptiles and of birds (see Figs. 109, 112; pp. 275, 280)—helps to approximate the ciliary body to the periphery of the lens. The 40-60 ciliary processes (Fig. 110, p. 277) have their crests firmly fused to the lens capsule (except in some or all marine forms). They send continuations a little way onto the iris.

The ciliary muscle fibers are mostly meridional in orientation. They originate from the inner layers of the substantia propria of the cornea and run close to the sclera to terminate in the connective tissue of the flat posterior zone (orbiculus) of the ciliary body. The muscle as a whole is small in land forms and terrapins, in which the sphincter iridis does most of the work of accommodation. But in marine turtles, which have not much needed to employ the iris muscle for deforming the lens (since they are limited to aquatic vision, and need no tremendous range of accommodation), the ciliary muscle is massive; and this is probably a primitive situation. The transversalis muscle (see pp. 269, 279, 299) originates in the connective tissue between the ciliary body and sclera, ventrally, and passes through a portion of the (otherwise healed) embryonic fissure of the pars cæca retinæ to pull on a group of zonule fibers which serve as its tendon. Its relationships are thus much like those of the amphibian's ventral protractor lentis, with which it is conceivably homologous.

The iris is not sharply demarcated from the ciliary body, since the base-plate of the latter is largely separated from the sclera and makes no sharp angle with the iris at the latter's periphery. Both retinal layers are pigmented, and it is doubtful whether the anterior layer ever gives rise to a dilatator comparable with that of the mammals. Radial muscle fibers may be seen even contiguous with the anterior retinal layer, but these are nucleated and are probably only re-oriented derivatives of the massive sphincter muscle, which occupies the whole breadth of the iris from pupil to root.

The lens is the softest, most pliable in the vertebrates. It is flattest in the tortoises (equatorial-axial diametral ratio 1.6 in *Testudo græca*), less flat (*ca.* 1.3) in terrapins, and virtually spherical in sea-turtles—where of course it need not be prepared to deform as much as in the other types of chelonians, but needs a strong curvature when at rest owing to the optical absence of the cornea. The 'ringwulst' is weakly developed in chelonians. The primary vitreous of the embryo is not

represented (as in fishes, amphibians, and other reptiles) by a broad funnel whose mouth coincides roughly with the retinal ora terminalis. Instead, there is a slender canal of fairly uniform diameter which runs forward from the disc, like the mammalian canal of Cloquet, but does not reach and touch the lens; rather, it ends on the anterior hyaloid membrane toward the temporal side (Fig. 175).

The vascular pattern of the eyeball, as worked out by Fritzberg on *Emys orbicularis,* compares quite closely with that of the frog. There are no vitreal vessels, however—their place was probably taken (physiologically) in primitive reptiles by the conus papillaris (p. 607); but no well-developed conus occurs in any known adult chelonian. In advanced embryos of *Chelonia, Chrysemys,* and *Chelydra,* a small, unpigmented, avascular glial cone forms upon the nerve head; but in the adults of these genera (except perhaps *Chelonia*), the surface of the 'disc' smoothly continues that of the surrounding retina. It is difficult to say why the turtles have been able to dispense with (or to avoid evolving?) a conus when the lizards have not, for the turtle retina is nearly as rich in cones; but the general difference in activity of turtles and lizards is perhaps the explanation (see p. 653). The poor development of the average chelonian chorioid strongly suggests that the metabolic requirements of the retina are relatively low.

The Retina—The retina is decidedly impure in its lamination (Fig. 176a), with every nuclear layer containing some elements which 'belong' at some other level. The horizontal cells have ropy processes, and may have reverted completely to a non-conductive function. All or nearly all chelonians have an area centralis. Outside of this, the visual:ganglion cell ratio is in the neighborhood of 2:1; but within the area there is of course a lower summation-ratio. A fovea has been claimed, and later authoritatively denied, for each of several genera; but such a feature has been convincingly demonstrated (by photomicrography) only in *Amyda* (by Gillett, who failed to realize the uniqueness of his discovery).

Prior to 1877, about everyone who described a chelonian retina saw rods in it, but since that time, owing to one of the few mistakes (and the weighty authority) of Max Schultze, the turtles have been placed among the pure-cone reptiles. They do however possess droplet-free elements with heavy, cylindrical outer segments, morphologically identical with the unquestionable (rhodopsin-containing) rods of crocodilians and with the plump peripheral rods of birds. It is not known whether these cells contain rhodopsin, but since they are most numerous in the

light-shunning turtles it is clear that they are physiologically rods, bearing several signs of cone ancestry (Fig. 176b and Plate I).

Rods are perhaps lacking in the foveate *Amyda* (Gillett figures only cones), but this form's suborder, the Trionychoidea, is not primitive, though characterized by a soft shell (so, secondarily). We may be sure that these droplet-free elements, serving originally as cones, were part of the cotylosaurs' equipment, though their origin (presumably from droplet-bearing cones) cannot be traced in any living vertebrates (Plate I). The other visual-cell types of the turtle group are the same droplet-bearing single and double cones which we have already seen in the amphibians and traced to the archaic Chondrostei (Fig. 176b; *cf.* Fig. 174a, p. 599).

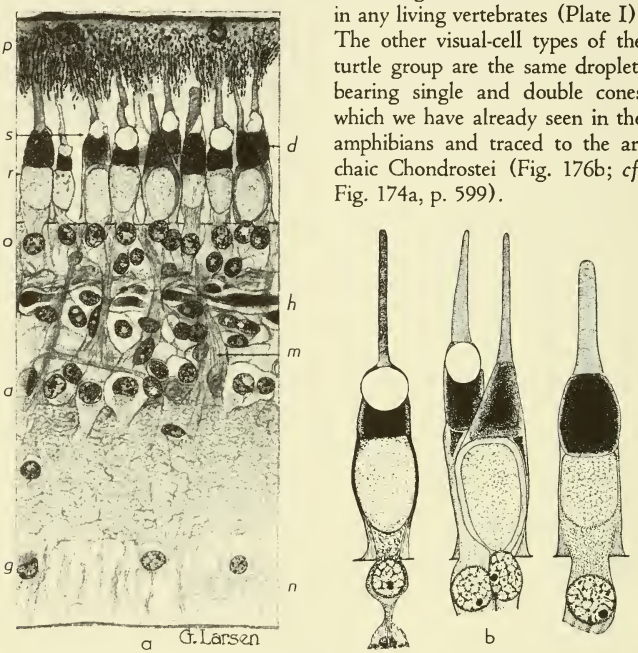

Fig. 176—The chelonian retina and its visual cells.

a, retina of common snapping turtle, *Chelydra serpentina*. ×500.
a- amacrine cells; *d*- double cone; *g*- ganglion cell; *h*- horizontal cells (ropy type); **m*- Müller fiber; *n*- bundle of nerve fibers; *o*- outer nuclear layer; *p*- pigment epithelium; *r*- rod; *s*- single cone.

b, single cone, double cone, and rod of *Chelydra serpentina*. ×1000.

(B) Crocodilians

See also pages:
135, 138 relationships
145, 543 habits
162, 224, 501 pupil
184 area centralis
202-3 oil-droplets
207 visual acuity
231, 238, 240 tapetum, eyeshine
251 Fig. 100
270, 274 sclera, ossicles
272-9, 436 accommodation, refraction
293 visual fields
305 eye movements
436 amphibious adaptations
496 vision, color vision
519 Fig. 156
542-3 dermal color changes
544 coloration of eye

The Eye as a Whole—In this small group of large reptiles the eyeball bears the stigmata of a long-continued nocturnality, which has affected every part of the organ. The specializations of the adnexa are directed toward the largely aquatic activities of the group (see pp. 421-2). The globe is of 'nocturnal' size, its diameter reaching 20mm. in the alligator and exceeding this value in larger types. The eye of the American alligator (*Alligator mississippiensis*) is better known than that of any other form; but nearly all the studies of it have been made by European investigators.

The sclera has retained the ancestral cartilaginous cup, but has lost the annulus of ossicles. Their disappearance has permitted the circumcorneal zone of the sclera to become convexly curved like the rest of the fibrous tunic. The eyeball is consequently practically a sphere, though a bit shortened axially. The cartilage reaches nearly to the ora terminalis, which lies a little in front of the equator. The purely fibrous tissue anterior to the cartilage is greatly thickened, but thins again before it coalesces with the substantia propria of the thin cornea.

The chorioid is thick and richly vascular behind the tapetum (*v.i.*), thin and poor in vessels elsewhere. The broad ciliary body shows—even more markedly—the same divergence of the base-plate (bearing the ciliary processes) from the muscular lamina (clinging to the sclera) which we noted in the turtles. The cleft thus formed at the periphery of the anterior chamber is filled by a wedge-shaped (in section) mass of loose connective tissue, the anteriormost strands of which run directly from the cornea to the root of the iris to form a pectinate ligament.* The much-branched canal of Schlemm does not, as in turtles, lie in this meshwork tissue, but is completely embedded in the thick contiguous sclera.

*For an analogous situation, see Figure 191, p. 645.

The loss of the scleral ossicles in these animals is coupled with a virtual disappearance of the ringwulst of the lens. These two losses are clearly related to the nocturnality of the crocodilians and their consequent lack of need of much or any accommodatory capacity. The evolutionary outbulging of the circumcorneal sclera upon the loss of its supporting bones, and the inward shrinkage of the lens equator owing to the thinning of the annular pad, have not however taken the ciliary body entirely out of contact with the lens (as these same changes have done in the mammals). In the crocodilians the hundred-or-more greatly elongated ciliary processes—they have been called 'tongue-like'—still contact the thick capsule of the lens at its equator; and according to Beer and Hess the accommodatory effort, though slight and exerted with extreme slowness, is still sufficient to pull inward the circumcorneal zone of the sclera and produce some bulging of the center of the rather flat anterior surface of the lens.* The (wholly meridional?) ciliary muscle lies in the sclerad lamina of the ciliary body, and is scarcely as well developed as in terrapins. Its fibers underlie the orbiculus, far distant from the limbus, with their anterior ends attached to the inner surface of the scleral thickening and their posterior insertions in the meshwork tissue close to the anterior border of the chorioid.

The accommodatory equipment centering around the ciliary muscle is thus at a low ebb in the crocodilians, as in the turtles—but not for the same reason: in the former, it is a logical consequence of an age-old nocturnality with its crude images and its indifference toward a precise focusing thereof, while in the turtles it is owing to the fact that the pupillary sphincter has taken on most of the work of increasing the curvatures and focusing power of the lens. The transversalis muscle, if ever present in early crocodilians, is apparently lacking in living species.

The deep pigmentation of the thick iris stroma is concealed in the living animal by an anteriormost layer of lipophores which gives the iris a lemon or cream color. The sphincter resembles that of turtles in that its fibers are distributed throughout the whole width of the iris, though concentrated only near the pupil. The posterior retinal layer is heavily pigmented and cuboidal. The anterior is squamous and unpigmented. It may be radially contractile; but it is generally denied that a dilatator is ever present in crocodilians—which may largely explain why the alligator's pupil is so slow to open (p. 501).

*The periphery of which surface only flattens the more during accommodation, being presumably kept from sharing in the 'bulge' by the pressure of the iris against it.

The Retina—The crocodilian retina is strongly 'nocturnal' in organization, and seems to have long ago lost any need for nutritive provisions other than the chorioid. At any rate, the only traces of a former conus papillaris (if indeed they *are* such remnants!) are a glial pad on the adult disc, which contains a capillary or two but scarcely protrudes toward the vitreous at all, and a superficial dusting thereof with melanin granules. The following remarks apply to the alligator:

The pigment epithelium is highly modified, in the superior half of the retinal cup, forming a guanin tapetum lucidum (*q.v.*). Toward the

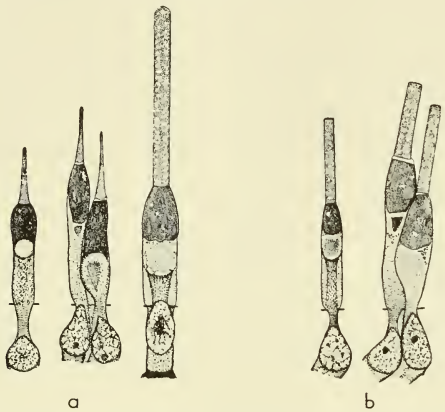

Fig. 177—Representative visual cells of a crocodilian, *Alligator mississippiensis*. ×1000.
a, single cone, double cone, and rod (the cones from the ventral fundus; the rod from the region of the tapetum lucidum).
b, single and double, partially-transmuted cones from opposite the center of the tapetum.

ventral border of the tapetalized area there is a horizontally-elongate area centralis, from which no attempt seems to have been made to eliminate the rods, though all the visual cells have here been slenderized and aggregated.

The horizontal cells are not quite as heavy-fibered as those of turtles; but the Müller fibers are particularly numerous and conspicuous. The extent of summation may be gathered from the fact that there are one to one and a half rows of outer nuclei, four to five rows of inner ones, and a single scattered row of ganglion-cell nuclei.

The types of visual cells (Fig. 177a) are the same three as in the turtles (*cf.* Fig. 176b, p. 612), and are respectively homologous with them (see Plate I). The oil-droplets have long since been discarded from the cones, however,* and the rods are rich in rhodopsin and greatly outnumber the cones, instead of constituting a minority of the visual cells as in even the most photophobic of chelonians.

In the region backed up by the tapetum, it might be expected that the cones would have become diminished in numbers or even eliminated, to make that much more room for sensitive rods. Instead, the cones have been retained; but their outer segments—even in the 'area centralis'—have been made as rod-like as possible (*i.e.*, heavy and cylindrical—Fig. 177b). Within this single retina we may thus observe a local, partial transmutation of cones into rods. These 'intermediate' visual cells are interestingly like the droplet-bearing elements of *Sphenodon* (Fig. 179, p. 621) in their morphology—and no doubt, to a degree, in their physiology.

(C) Sphenodon

See also pages:
78 rhodopsin
135, 138 relationships
189-90 Fig. 82, visual cells, fovea
200-2 oil-droplets
206 vision
216 visual cells
224 pupil
251 Fig. 100
274 scleral ossicles
339-40 parietal eye
497, 519-20 color vision

This single living member of the Rhynchocephalia was originally thought to be a lizard, and was placed in the lacertilian family Agamidæ. Its true nature transpired at a time when the rhynchocephalians were supposed to be very primitive. Anatomically, *Sphenodon* is indeed 'generalized' as compared with the highly specialized—though far older—chelonians and crocodilians. But its position in modern taxonomy is near the lizards.

All sorts of efforts have been made to see the *Sphenodon* eye as the 'most primitive' sauropsidan optic; but it is nothing of the kind. So far as the eye is concerned, *Sphenodon* can best be described as a pre-lizard which has gone off the beaten track into nocturnality.

*In *Alligator* and perhaps in all; but mentions of colorless oil-droplets (in unnamed species!) occur in even recent literature.

The Eye as a Whole—The adnexa bear closer resemblance to those of lizards than to those of amphibians or other reptiles (see pp. 420-3, Fig. 143 on p. 421). The lacrimal gland can be lacking in a lizard (as it is in *Sphenodon*). The nictitans tendon attaches to the orbital wall in *Sphenodon* as in lizards; and the nictitans musculatures are mutually convertible. The two-headed retractor bulbi of *Sphenodon* is the largest of the extra-ocular muscles, and is innervated not only by a branch of the sixth cranial (abducens) nerve but also by a sprig from the ciliary ganglion.

The eyeball has been described in its entirety only by Osawa (1898), who made certain errors and oversights. It is large for the size of the animal (as compared with a diurnal lizard), with an equatorial diameter of 17mm. and a slightly shorter axis. A considerable change in surface curvature takes place at the limbus, creating a sclero-corneal sulcus (which, it will be remembered, we have not seen in any forms below *Sphenodon,* but which we will encounter regularly hereafter).

The sclera contains a cartilaginous cup, and, including the fibrous layer outside of this, is about as thick as the retina. Anteriorly the cartilage extends about to the ora terminalis, and is there overlapped slightly (externally) by the circlet of scleral ossicles.* These agree in number (16-17) better with those of lizards (12-15) than with those of turtles (6-11). The cornea is strongly arched, of uniform thickness throughout, and is 9.5mm. in diameter—the same size as that of an *Iguana* eye of the same diameter, but relatively large as compared with that of such a sun-worshipping diurnal lizard as the deserticolous *Uromastix* (eye 12mm., cornea 3.4). The cornea has a thin epithelium (consisting of only two layers of cuboidal cells with round nuclei), Descemet layers, and a thick propria which contains no such vertical fibers as are described by Osawa. The inner layers of its fibers, at the margin of the cornea, blend into a narrow thickened zone of the sclera which lies opposite the iris root.

The chorioid is especially heavily pigmented on its scleral side. It is thicker than in small-eyed lizards (but no thicker than in, say, *Varanus*), and is well vascularized. Grouped and scattered in it are peculiar spheroidal pigment cells with central nuclei suspended by delicate protoplasmic strands, as in a brown-fat cell. These cells form a dense aggregation opposite the fovea (not visible, owing to bleaching, in Fig. 82 on p. 189). The glass membrane can be easily followed through the ciliary body (where it is greatly thickened), but not into the iris; and the choriocapillaris also extends well into the ciliary region.

*Not obvious (*e.g.,* Fig. 178) unless section passes through center of ossicle.

The ciliary body increases gradually in thickness from behind forwards, from near-equality with the chorioid to about twice this value. Its base-plate and epithelium do not, however, diverge widely from the sclera, so that only a small amount of spongy tissue lies between (Fig. 178; contrast Fig. 191, p. 645). Osawa to the contrary, there are no ciliary folds or processes—the inner surface of the broad ciliary body is perfectly smooth, which seems an important point in agreement with the lizards. Where the ciliary body joins the iris, there is a sharp 'corner' or

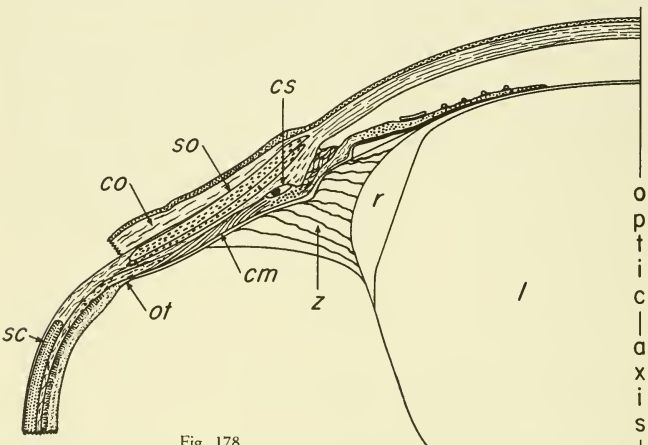

Fig. 178

The anterior segment of *Sphenodon punctatum*. × 12. *cm-* ciliary muscle (anterior, circumferential fibers show as a group of dots beneath the canal of Schlemm); *co-* conjunctiva; *cs-* canal of Schlemm (containing nerve, shown in black); *l-* lens; *ot-* ora terminalis; *r-* ringwulst; *sc-* scleral cartilage; *so-* scleral ossicles; *z-* zonule.

annular ridge, from the crest of which a delicate, elastic, radially fibrous cuticular membrane—actually, the anteriormost 'leaf' of the zonule—passes straight to the posterior surface of the iris which it intersects at about one-third of the way from iris root to pupil. Here it is as firmly fused with the iris as with the lens capsule; and, if the lens and iris are separated (in preserved eyes, at least), it remains attached to the iris rather than to the lens. The zone of the iris thus bridged by this membrane has a rugose posterior surface on which the low, undulant folds

run roughly radially; but these could hardly be called iris folds (*e.g.,* in the anuran sense).

The bridge-membrane, besides contributing to the anchorage of the lens, probably helps to hold the iris against the periphery of the anterior surface of the lens during accommodation—if any—by using the iris as a third-class lever, thus confining the accommodatory deformation of the lens surface to the portion behind the pupil (see footnote, p. 614).

Gross dissection reveals what is apparently a transversalis muscle; but this lacks histological confirmation as yet.

In the loose meshwork of the ciliary body, the most conspicuous structure is the enormous canal of Schlemm, which lies at the inner side of the sclera just behind the thickening at the iris root. Toward its posterior side there is a large annular nerve, as in most lizards. The canal is supposed to be lacking in *Sphenodon* (but Osawa was looking for it in the sclera, where it seldom lies in reptiles; and his drawing shows it plainly —unlabelled—in its true location). The ciliary muscle is relatively weak. It does not commence at the anterior end of the ciliary zone, but about a quarter of the way back. Its fibers originate partly upon scleral tissue lying behind the iris-root thickening, partly from the inner surface of the sclera paralleling the posterior half of the ciliary body, and insert into the connective tissue of the orbicular base-plate and on the outer surface of the glass membrane in that region, a very few of them all the way back to the ora terminalis. In horizontal sections of the eye, the anteriormost ciliary-muscle fibers on one side of the eye are seen to be cut in cross-section (*cf.* such lizards as *Seps* and *Lacerta;* p. 624).

According to Ida Mann the iris is covered anteriorly by a layer of chocolate chromatophores, through breaks in which some coppery and silvery-buff patches of deep-lying iridocytes can be seen in the living animal. The blood vessels form a system of arcades aimed inward toward the pupil, and many of them form loops which burst free of the iris surface into the anterior chamber. This iridic circulatory pattern resembles those of crocodilians and geckoes about equally well.* Muscle fibers with a sphinctral function are evenly distributed throughout the stroma from pupil to iris root; but they are concentrated toward the periphery since the iris is thickest here and thins gradually toward the pupil. The dilatator fibers lie against the epithelial retinal layers. It is clear that they are direct derivatives of the sphincter (as perhaps in all

*Unfortunately, the vascular pattern of the whole eye of *Sphenodon* has never been worked out.

reptiles), and not parts of the underlying anterior-epithelial cells as are the dilatator elements of mammals. Both retinal layers (as in lizards) are heavily pigmented—the anterior, even more so than the posterior (as in all vertebrates in which a dilatator is lacking or, if present, is not formed as a lamina of the anterior retinal layer).

The anterior chamber is very shallow and the lens is large—8.0mm. × 6.33mm.—in keeping with the nocturnal habits of the animal. Thus, the quotient of eye diameter and lens diameter (17/8) is 2.12 in *Sphenodon,* 2.7 in *Iguana,* and 2.78 in *Uromastix* (*cf.* corneal proportions, above). The flatness-index of the lens (8/6.33) is 1.26, while the lenses of diurnal lizards average somewhat flatter (1.4-1.5) and that of a terrestrial turtle (*Testudo græca*) is flatter still (1.6). The alligator lens is about as rotund as that of *Sphenodon,* however (1.25), and nocturnal lizards (geckoes) have nearly spherical lenses (*e.g., Tarentola mauretanica*—1.1). The *Sphenodon* eye may perhaps have a relatively large retinal image for a nocturnal animal; but this is not out of line with its retention of other features having to do with the maintenance of good resolution—the fovea, for instance, as well as some of the sauropsidan adjuncts to good accommodation (scleral ossicles, ringwulst). The anterior surface of the lens is much less sharply curved than the posterior, and the ringwulst is well developed, its thickness being 6% of the diameter of the whole lens.

There are no vitreal vessels; and there is no conus papillaris—and even less trace of one than in the crocodilians, for the optic disc is not even convex, and shows only a very few melanin granules. The disc is slightly temporal and considerably ventral in position, its center lying about 2.5mm. from that of the exactly (?) central fovea. The sensory retina, as in large lizard eyes, tapers gradually in thickness anteriorly, so that the ora is not abrupt. The optic nerve is relatively slender, with a simple circular cross-section, and entirely lacks any septal system. Elsewhere in the reptiles, so simple a situation occurs only in the (also nocturnal) crocodilians.

The Retina—Because of the coarseness of its visual-cell mosaic and its Müller fibers (which become massive in the far periphery, and occupy most of the volume of the retina there), the *Sphenodon* retina appears at first glance to resemble that of the turtles. Closer analysis shows that the strongest similarities are to the lizards. *Sphenodon* has a concaviclivate fovea (Fig. 82, p. 189), which in the diurnal ancestor was probably entirely lizard-like.

The visual cells (Fig. 179; *cf.* Figs. 176b, 177a, 181; pp. 612, 615, 626) clearly explain the persistence of the fovea, which has been lost in other nocturnal reptiles whose diurnal relatives are foveate (*e.g.*, geckoes, xantusiids, pygopodids). The matching single and double elements are about equal in numbers and greatly predominant. They are manifestly homologous with the single and double cones of turtles and crocodilians; but *Sphenodon* has converted them into physiological rods by enlarging their outer segments and largely bleaching their oil-droplets—which, however, have been retained (contrast Fig. 177b, p. 615).

The third, tiny type of element is very scanty. Never more than twenty can be counted in a 10μ sagittal section of the large (17mm.) eye. It is an unmodified droplet-free cone, obviously useless to the animal and on its way to total disappearance. By reference to Plate I, it will be seen that this element must be the same cotylosaurian-eosuchian droplet-free cone which has become a rod in the turtles and, independently, in crocodilians (and still once more in the birds or in their dinosaurian ancestors—see p. 661). It seems thus to be a little-cone-which-makes-a-better-rod. Why, in converting over to nocturnality, *Sphenodon* elected instead the two droplet-bearing elements for transmutation into rods, cannot be explained. But the droplet-free element has obviously proven unsatisfactory in modern reptiles as a cone—not only to *Sphenodon,* where it is even excluded from the fovea—ordinarily a pure-cone region in other vertebrates (not one shows in the field of the photograph in Fig. 82, p. 189)—but also in the lizards, which eliminated it entirely (see Fig. 180a, p. 626).

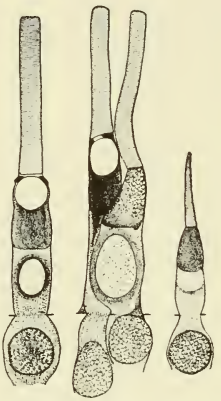

Fig. 179—Representative visual cells of *Sphenodon punctatum*: single rod, double rod, and cone. × 1000.

Sphenodon very probably owes its long survival as a 'living fossil' to its adoption of nocturnality, which was facilitated by the transmutation of diurnal-ancestral cones into low-threshold elements, and expresses itself elsewhere in the eye in the simplified optic nerve, the slit pupil, the shallowed fovea, the enlarged lens (and cornea), the loss of the conus papillaris (see p. 653), and the reduced accommodatory apparatus.

(D) Squamates

See also pages:
56, 61-3, 161-2, 165-8, 176, 178, 216, 254 visual cells, transmutation
72, 169-70, 206 vision
78 rhodopsin
101-2 zapfensubstanz
134-5, 138 origin, relationships
145, 215, 342 habits
157, 161-2, 220-1, 224-5, 256-7 pupil
174 acuity adaptations
185-8 fovea
191-6, 199-203 yellow filters and their significance
223 Fig. 88
230 eyeshine
251 Figs. 99, 100
254, 270, 272-3, 279-83, 438, accommodation, refraction
270-1, 274 scleral ossicles
289, 293-5, 321 visual fields
299-300 binocularity
306-7 eye movements
339-40 parietal eye
344-5 movement perception
423-4 adnexa
438 amphibious adaptations
450-1, 454-9 spectacle
465-7, 495-7, 519-20 color vision
524-6, 538-43 dermal color changes
545-9 coloration of eye

The twenty families of lizards and the eleven families of snakes are scattered around the globe in the temperate and torrid zones. Nothing in biology is more certain than that the snakes were derived from lizards, and the closeness of the relationship is indicated by the placement of the two groups in a single order, the Squamata (meaning 'with scales') as suborders, the Lacertilia (lizards) and the Ophidia (snakes).

Lizards—The lizards exhibit a greater number of the ocular features listed earlier as 'reptilian' than do any other living reptiles. This does not mean however that this combination of features was evolved first by this relatively recent group—the absence of certain of them in turtles, crocodilians, and *Sphenodon* has been explained above as owing to secondary nocturnality, to a special importance of the iris in accommodation, etc. We may be sure that the lizards have only *preserved,* not assembled, the complex here characterized (pp. 607-8) as 'reptilian'; for, we shall encounter the entire complex again in the birds, which got it not from the lizards, but from much older reptiles—the ornithischian dinosaurs which were the birds' immediate ancestors.

The lacertilian eye is relatively large and characteristically 'diurnal' in make-up, and has certainly been so for as long as there have been lizards—and longer: If we could take the eye of *Sphenodon* in hand and undo all of the things which have been done to make it suitable for dim-light activity, we should find ourselves holding an essentially lacertilian eye, representing not only the eye of the ancient diurnal rhynchocephalians but probably that of the eosuchians as well (see Fig. 60, p.

135). To make complete the identity between the 'diurnalized' eye of *Sphenodon* and that of the lizard, we should need only to pluck the droplet-free cones from the *Sphenodon* retina.

The adnexa have been described adequately elsewhere (p. 423). The eyeball is as high as it is wide except in the largest lizards, where it has some horizontal ellipsoidality. The axial length is shortened somewhat, and in diurnal species the circumcorneal region of the sclera is more or less concave—supported so by the *ca.* 14 scleral ossicles, as part of the means by which the ciliary body and the lens are brought into contact for the purposes of accommodation. The thin scleral cartilage usually reaches forward at least to the equator, often beyond, where it is met (or a bit overlapped) by the broad, thin, ossicular ring (Fig. 182, p. 632). In the chameleon, however, the cartilage is reduced to a four-millimeter disc which lies behind the foveal region.

The circular cornea is usually of uniform thickness throughout its arch (*cf. Sphenodon*), and is relatively thin in large eyes, relatively thick in small ones. Its sharp curvature continues for a little way into the ossicular zone, before the sigmoid flexure of the ossicles reverses the curvature to become the more gentle one of the posterior segment. The usual layers are present except in some geckoes, where (*e.g.*, in *Hemidactylus mabouia*) there is no trace of Descemet's membrane or mesothelium.* At its margin, the corneal substantia propria separates briefly into three laminæ, the two outermost becoming the fibrous investment and lining of the ossicular zone of the sclera, while the innermost blends with the connective tissue of the iris-angle region and often serves as the 'tendon' of the ciliary muscle.

Except in the smallest eyes, the retina thins out very gradually toward the ora terminalis (as in *Sphenodon*), where the thin chorioid becomes the ciliary body. This is very broad owing to the disparity between the size of the posterior segment and that of the cornea. The base-plate diverges slowly from the sclera, so that even at its anterior end the ciliary body is not very thick (compare *Sphenodon;* contrast chelonians and crocodilians). The anteriormost strands of the meshwork tissue of the iris angle may be organized as a pectinate ligament, but this is never as well defined as in birds. There are no ciliary processes. Nevertheless, the ciliary body has a broad zone of firm contact with the lens, which is

*Present, however, in *Coleonyx*—as one of the many reasons (ophthalmological ones, at least) for considering this and other 'eublepharid' geckoes to be a distinct group with perhaps only very distant kinship with the spectacled majority of geckoes.

thus directly squeezed equatorially when the ciliary muscle contracts and moves the anterior end of the ciliary body forward and axiad (see Fig. 109, p. 275, and Fig. 182, p. 632).

The ciliary muscles show great variations from lizard to lizard. Typically, perhaps, they are as described on pp. 277-80; but they are often much simpler. In the Teiidæ, for example, the muscle is all in one piece, its purely meridional fibers originating from the corneal margin (*v.s.*) and terminating in the base-plate and on the glass membrane. In nocturnal forms, the muscle may be massive or it may be greatly atrophied as if the animal had abandoned all attempts to accommodate. The muscle is tiny in *Xantusia riversiana* and in *Hemidactylus mabouia,* and absent in *X. henshawi, X. vigilis,* and *Heloderma suspectum.* It is huge in *Coleonyx variegatus,* however, and is well developed in *Aniella pulchra* considering the size of the eye. There are often special arrangements which seem purposed to produce a nasad shift of the lens during accommodation, thus aiding the transversalis muscle (usually present) in converging the visual axes. Thus in *Seps* and *Lacerta,* bundles of circumferential fibers have been described and figured in the temporal half of the eye (*cf. Sphenodon*); and in *Tupinambis,* though all the fibers are meridional, they are much longer on the temporal side.

The iris is relatively thick, and often thicker toward the pupil, where there is a vascular plexus fed by a temporal and an inferior artery and drained by many radial veins. The sphincter is scattered through the whole iris, and some of its fibers are bowed into radial positions and must act separately, since no other dilatator is present. Where the pupil is a vertical slit, the arrangement may be very complicated (see Fig. 88e, p. 223). Both retinal layers are deeply pigmented. The zonule is very thick where it attaches to the lens, and its anteriormost laminæ run parallel to the iris and so close to it that they suggest the origin of the 'bridge-membrane' of *Sphenodon.*

The lens has an extremely thin capsule and is very soft, though not so much so as in turtles. Its 'ringwulst' or annular pad is relatively thick —in the chameleons, the thickest known. In the diurnal majority the lens is flatter than in any other reptiles. The primary vitreous forms a broad funnel, indicating that the slender hyaloid canal seen in turtles—though these are the most primitive of living reptiles—is something special.

Pointing through the watery vitreous toward the heart of the lens is the conus papillaris, a slender papilla rooted on the ventro-temporal optic nerve head (Fig. 182, p. 632). It consists largely of tiny blood vessels

with their surfaces heavily dusted with pigment granules, and among these just enough neuroglial tissue to hold the whole together and in shape. In cross-section the conus may be circular, oval, X- or Y-shaped—in the latter cases, foreshadowing the buttressed 'pecten' of the lower birds. It is supplied by an artery and a vein which reach it through the optic nerve, and is one of the various devices which many vertebrate eyes have found necessary for supplementing the disadvantageously-located chorioid in the nutrition of the inner layers of the retina (see pp. 648-58).

In profile the conus may be stubby, long and nearly cylindrical, or dagger-like. In length, it varies from a nubbin in most nocturnal forms (*Xantusia,* many geckoes) and sluggish species (skinks) to a third or more of the diameter of the eyeball—in such instances, nearly reaching the lens. It is completely lacking only in the various families of worm-like, burrowing lizards (Amphisbænidæ, Euchirotidæ, Anelytropidæ, Dibamidæ*), whose tiny (less than 1.0mm.) eyes are buried beneath (usually) opaque skin and seldom consist of more than a connective-tissue capsule containing an optic cup and a lens.

The Lacertilian Retina—The outstanding feature of the retina is its fovea centralis, which is not known to be lacking in any diurnal lizard. The fovea may, as in chameleons, be larger than that of man, and with a vastly greater concentration of visual cells (as many as 756,000/sq. mm.). The fovea is absent, despite statements to the contrary, in all geckoes which have ever been examined; and it is also wholly lacking in pygopodids, *Heloderma,* and most xantusiids. In *Xantusia vigilis,* however, just enough trace of an area centralis has survived the family's adoption of nocturnality to enable one to tell where in the retina the fovea used to lie. The disturbance created in the average lizard eye by the fovea scarcely finds scope to subside before the ora terminalis is reached (see chameleon in Fig. 71, p. 173), and it is only in monitors, iguanas, and the like that the retina has sufficient area to boast a wholly unaffected 'extra-macular' peripheral zone of any great width.

In its laminal purity and in the thickness of its inner-nuclear and ganglion layers, the lacertilian retina is exceeded only (and not greatly) by the visually supreme birds. The pigment-epithelial processes are

*But not *Aniella.* The eyes of this little Californian worm-lizard are a little less than a millimeter in diameter, but they have all their 'works'—pigmented conus, normal retina and visual cells, scleral ossicles, ciliary muscle, ringwulst etc. This genus is erroneously listed in Table XI (p. 450) as having a spectacle. The lids are mobile, despite statements to the contrary in herpetological literature.

numerous, long, and fine, but the pigment migrates so slightly that it forms practically permanent sheaths around the individual cone outer segments, as in diurnal snakes.

The visual cells are always of two types (each varying, of course, in size), which form a 'matching' single-double combination (Fig. 180).

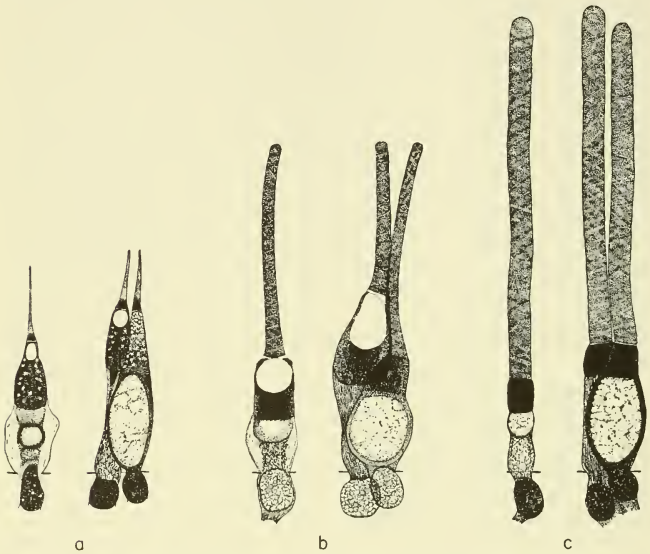

Fig. 180—Visual-cell types in representative lizards. ×1000.

a, single and double cones of a diurnal lizard, *Crotaphytus collaris*.

b, single and double 'intermediate' elements of *Xantusia riversiana*.

c, single and double, completely transmuted rods of a gecko, *Coleonyx variegatus*.

In the diurnal majority of families both of them are typical cones (Fig. 180a) with yellow oil-droplets, respectively homologous with the droplet-bearing single and double elements of all lower reptiles and the birds and lower mammals—indeed, tracing their ancestry back to the chondrostean fishes (see Plate I). In the nocturnal 'leaf-footed'- or snake-lizards (Pygopodidæ) of Australia, however, the oil-droplets have been discarded and the outer segments somewhat enlarged to permit scotopic

vision. In *Aniella* and *Heloderma* the droplets are present though colorless—which is true also of *Xantusia,* whose outer segments are rod-like in size and shape (Fig. 180b). The geckoes have finished the job of changing the ancestral cones into rods, whose outer segments contain an abundance of rhodopsin and are either very long and slim as in *Coleonyx* (Fig. 180c), or short and thick as in the spectacled geckoes.

A few genera of geckoes have secondarily (or tertiarily!) reverted to round pupils and partial or perfect diurnality. These include *Phelsuma, Lygodactylus, Pristurus, Gonatodes, Microscalabotes, Sphærodactylus* (some spp.), and perhaps *Teratolepis.* All of these are candidates for histological examination, which in some of them at least will unquestionably reveal that the visual cells have become 'cones' once more.

Snakes—Leaving out of account the 'blind' families (Typhlopidæ and Leptotyphlopidæ), in which the eye is tiny and vestigial, the eyes of snakes are quite thoroughly standardized in structure. From genus to genus (usually without regard to family boundaries) only minor variations occur, the most important of these being in the structure of the retina, in the shape of the pupil, and in the relative size of the lens—variations which, in short, are the bases of simple differences in visual habits with respect to light intensity.

The presence of the spectacle cannot be held accountable for the peculiarities of the eyeball other than the thin-ness of the corneal epithelium. And these peculiarities are numerous and great: as the ensuing description of the eyeball unfolds, the student who has just read the preceding portions of this chapter will not recognize the snake eye as a 'reptilian' one at all; but, under a subsequent heading, an explanation of the unique ophidian pattern will be offered which, it is believed, will be entirely satisfactory.

The eyeball in life is spherical or even a trifle elongated axially. The sclera is composed entirely of tendinous connective tissue. It is thickest posteriorly, where, in average-sized eyes, it about equals the retina. In the largest snakes (large boas, pythons) it is still thicker—up to one and one-half times the thickness of the retina (*e.g., Epicrates*). In very small eyes, however, the sclera is usually very thin. The equatorial zone, where the eyeball wall deforms most during accommodation, is almost always (exception: *Acanthophis*) the thinnest portion of the sclera. It begins to thicken again, as one passes forward, about at the ora terminalis, in front of which it is quite thick for a little space, then thinned again at its junction with the cornea. The outer surface of the sclera is usually

dotted with melanophores, and in a few instances these form a continuous thin layer of dense pigment (*Lichanura, Sonora, Abastor, Farancia, Natrix, Acanthophis*). In *Python* (*molurus*) there are also many flat pigment cells at various levels in the scleral tissue itself.

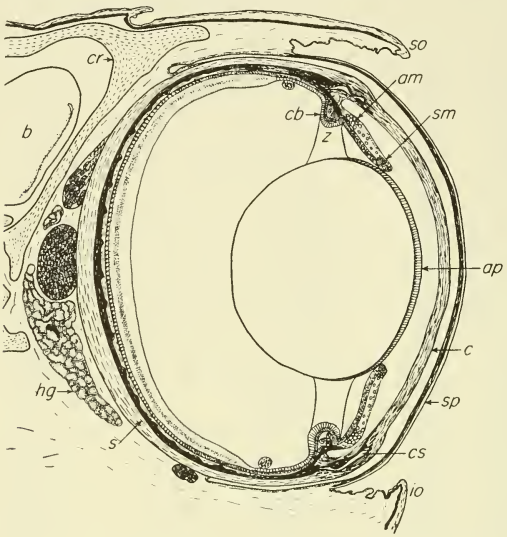

Fig. 181—The ophidian eye in vertical section: *Natrix natrix*. ×22. Redrawn from Schwarz-Karsten, modified from original preparations.

am- accommodatory muscle; *ap*- anterior pad of lens; *b*- brain; *c*- cornea; *cb*- ciliary body (main portion, the ciliary roll; note cross-section of hyaloid vein lying on orbiculus behind it; the very small vessels of the hyaloid plexus, lying on the inner surface of the retina, are omitted from the drawing); *cr*- cranium; *cs*- canal of Schlemm; *hg*- Harderian gland; *io*- infraocular scale; *s*- sclera; *sm*- sphincter muscle; *so*- supraocular scale; *sp*- spectacle; *z*- zonule (collapsed; see text).

The cornea is strongly arched and of almost uniform thickness except —usually—toward its margin, where it is markedly thickened (the 'corneal thickening' hereinafter mentioned). This thickening is lacking in many small eyes with thin scleras (*e.g., Charina, Phyllorhynchus, Hypsiglena, Trimorphodon*), and even in the presence of a relatively thick sclera, as in *Tropidophis* (where the peripheral zone of the cornea is actually thinned) and *Eryx*.

The chorioid is extremely thin (except in the limicolous 'rainbow snakes', *Farancia* and *Abastor*), consisting of little more than a choriocapillaris (with no large-vessel layer) and a few tightly-packed layers of pigment cells external to it. In contrast to other reptiles, the chorioid and sclera are firmly fused, as if they had never completed their embryological differentiation from each other.

Anterior to the ora, the chorioid continues unchanged (including its choriocapillaris) for a short space, where it is lined with the flat zone of the tall ciliary epithelium. This 'orbicular' zone is always very narrow (except in *Python* and *Epicrates*), and upon it lies an annular 'hyaloid' vein (except in boas; present, however, in *Python*). The orbicular zone itself is lacking in *Charina* and *Constrictor* (=*Boa*), and much reduced in *Lichanura*. Immediately in front of the ora in these snakes, and anterior to the orbiculus in all others, lies the ciliary body proper, which from its shape (Fig. 181) is perhaps best called the 'ciliary roll'. It forms an annular fold, consisting of the two tall columnar layers of ciliary epithelium with a core of deeply pigmented uveal tissue containing small blood vessels. From this core, strands of connective tissue sweep forward onto the inner surface of the cornea, petering out on the posterior slope of the corneal thickening. These strands have much the same relationships as those which compose the corneal meshwork tissue of man (see Fig. 5, *mt;* p. 10), which is so often mistakenly called a 'pectinate ligament': in both snake and man, the direction of these fibers is exactly at right angles to that of a true pectinate ligament (see Fig. 109, *pl;* p. 275).

The ciliary roll serves for the attachment of the zonule (*v.i.*), and is often taller and thinner (and sometimes sharp-edged) on the nasal side. In *Python* and the larger boas (*Constrictor, Epicrates*) it has this shelf-like character throughout its circular course.

In the Colubridæ and all of the higher families derived from them, the standard location of the venous canal of Schlemm is in the cornea, toward the rear of the corneal thickening. It may be separated from the anterior chamber only by the 'pectinate ligament' (*cf.* man!), but most often it lies completely surrounded by dense fibrous tissue. It sometimes branches (the branches then recombining) along its course and the secondary canals thus formed lie farther posteriorly, often in the core of the ciliary roll. Its connections are chiefly if not solely with the choriocapillaris of the orbiculus. The Boidæ show more variation: in *Constrictor* and *Eryx* no canal can be made out at all, and *Lichanura, Trop-*

idophis, Charina, and *Epicrates* have it as in the colubrids; but in *Python* it is located closer to the outer surface of the cornea than to the inner, and its connections are to the conjunctival veins.

The iris is fairly thick, with a highly irregular anterior surface. Its stroma contains not only melanophores as usual, but often guanophores and lipophores as well. The circulation is totally different from that in lizards (p. 624), consisting of a plexus occupying the whole iris, in which the small vessels cannot be identified as veins or arteries. The striated iris musculature is entirely mesodermal, and derived phylogenetically and embryologically from the ciliary region. Most of the fibers are circular in direction, and most of these are gathered into two accumulations, one near the pupil and serving as the sphincter pupillæ, and the other toward the root of the iris and acting as the muscle of accommodation. Some of the fibers of this latter muscle may be pressed back into the ciliary roll. The dilatator fibers underlie the sphinctral masses, and may also occasionally reach back into the ciliary roll (*e.g.,* in *Acanthophis*). In diurnal snakes the pupil has a peculiar, special duty owing to the absence of movable lids: during sleep it constricts, to facilitate visual unconsciousness.

The lens, unlike that of lizards, has sutures; and it lacks the ringwulst of other sauropsidans. Consequently it is not much flattened, and is helped toward its subsphericity (flatness index 1.1—1.25) by an 'anterior pad' except in *Eryx* and *Charina* (and perhaps all other boïds, or at least the fossorial ones). Like a ringwulst, the anterior pad is simply a region of the lens epithelium in which the cells are extremely tall instead of cuboidal. Except in water snakes, whose lenses deform somewhat during accommodation as well as moving forward, the lenses of snakes are firmer than those of lizards or turtles.

The zonule is peculiar, and perhaps variable, in organization. In its fullest development it consists of two radially-fibrous membranes. One of these arises from the front of the ciliary roll and passes along the back of the iris and over the face of the lens. The other is essentially equivalent to an anterior hyaloid membrane of the vitreous, and arises from the back of the ciliary roll and surrounds the back of the lens. This posterior 'leaf' is readily seen in some snakes (*e.g., Bitis, Coronella, Arizona*), but in many it can be made out with difficulty or not at all. The anterior 'leaf' would appear to function chiefly in hauling the lens promptly backward to its resting position upon the relaxation of accom-

modation (see pp. 282-3).* Since the back of the lens rests solidly against the cupped vitreous, it would not seem to matter whether the anterior limiting membrane of the latter flares out to attach to the ciliary roll (forming a 'posterior leaf' for the 'zonule') or coincides—as apparently it often (or usually) does, with the anterior leaf. Where two leaves are discriminable, there are practically never any other zonule fibers to be seen between them, with attachments to the equatorial region of the lens. A conspicuous exception however is *Epicrates*.

All snakes have a plexus of tiny blood vessels on the inner surface of the retina,† fed by an artery which enters through the optic nerve, and drained by the nasal and temporal arcs of the hyaloid vein (lying on the orbiculus) into a mid-ventral trunk which passes back over the surface of the retina to leave the globe through the optic nerve. This vein and artery are clearly homologous with those which, in lizards, supply the conus papillaris. And, in scattered members of every good-eyed family of snakes, they supply a conus as well as a network of vitreal vessels. But the 'conus' of these snakes has no genetic connection with the conus or pecten of other sauropsidans, for its framework consists of mesodermal connective tissue—not of neuroglia. It is never large or dagger-like, but most often forms a low mound, pigmented or clear, with a brush of cuticular fibers which emanate from it in all directions to disappear in the vitreous. It is longest and slenderest in *Vipera berus* (where it is heavily pigmented) and *Lampropeltis triangulum* (where it is colorless); but it is never relatively longer than the conus of a nocturnal lizard. The history of the ophidian 'conus' is best illuminated by the fact that it is frequently much larger in embryos than in their adults, and is often present in embryos whose adults lack all traces of it. Moreover, the development of the vitreal vessels goes hand in hand with the ontogenetic retrogression of the conus: as the latter dwindles, the mesoderm of its flared base creeps out on the surface of the retina, centrifugally from the optic nerve head, and it is in this film of mesoderm that the hyaloid plexus takes form. The embryological history of the conus-artery is thus strikingly like that of the mammalian hyaloid (see p. 113 and Fig. 42a, p. 112).

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*In life, the two leaves of the zonule diverge much more, toward the lens, than they are shown doing in Figure 181 (p. 628).

†In *Tarbophis*, these vessels are really embedded in the retinal tissue—some of them, quite deeply, as in mammals.

The ophidian optic nerve is unique—for the Sauropsida—in its total resemblance to that of *Neoceratodus* (p. 591). The lacertilian nerve is also fascicular, but its bundles lack ependymal cores and have more glial tissue between them.

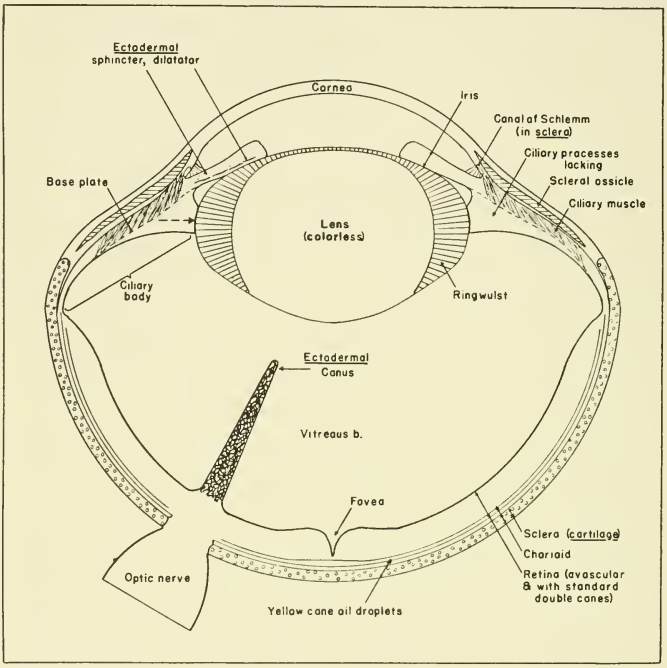


Fig. 182—Lizard eye, diagrammatic, for comparison with that of snake. (The dotted arrow shows the direction of application of the force of accommodation).

The History of the Snake Eye—If the reader needs any reminder of the magnitude of the difference between the snake eye and that of the ancestral lizard, it will be furnished by Figures 182 and 183. Herpetologists and palæontologists are agreed that the snakes originated from the stem of the lizard family Varanidæ, the 'monitors'. These are the largest of all lizards, and include the twelve-foot dragon of Komodo.

The largest snakes—including the monster of them all, the 35-foot regal python—are in the most 'primitive' family, the Boidæ.

If big monitors had simply 'become' big snakes, there would have been no need whatever for such a rebuilding of the eye as has occurred in the

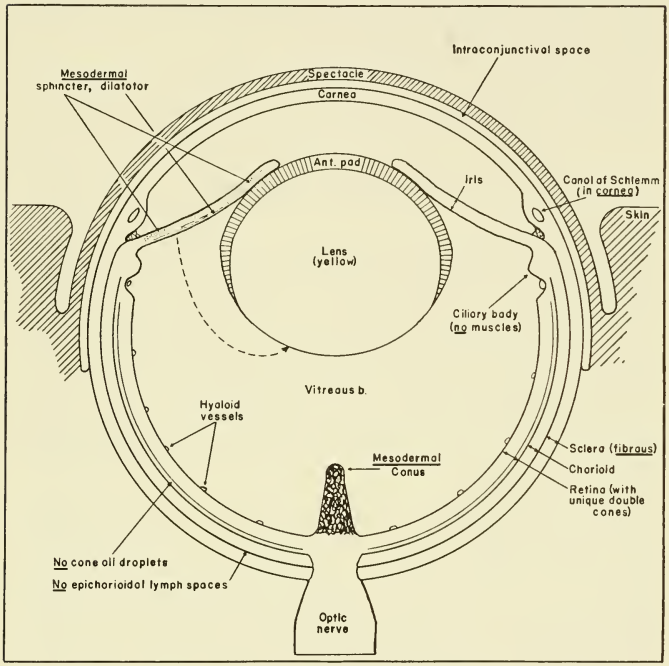


Fig. 183—Snake eye, diagrammatic, for comparison with that of lizard. (The dotted arrow shows the direction of application of the force of accommodation).

Ophidia. The modern snakes would have done just as well with unmodified lacertilian eyes as have the various imitation snakes—the legless above-ground lizards such as our *Ophisaurus ventralis* and the European *Anguis fragilis*. Earlier in this volume it was noted that the universal presence of the spectacle, in snakes of all habits and habitats, could only mean that the first snakes so lived as to require a spectacle: they were

either nocturnal, or else lived underground, and those of their descendants which are neither nocturnal nor fossorial have been unable to trade the spectacle in for a pair of mobile lids. Again, the absence of retinal oil-droplets in all snakes, and the presence instead of a yellow lens in diurnal species, has been emphasized as indicating that the early snakes shunned bright light. Their invention of the spectacle and their discard of the oil-droplets had a common basis.

Mere above-ground nocturnality would not, however, have called for any greater changes in the ancestral lizard eye than have occurred in the night-lizards, snake-lizards, and geckoes. The pattern of the whole snake eye is consistent only with the hypothesis that the first snakes lived underground or originated there from lizards which had become fossorial. Two whole families of snakes and several families of lizards have this habit even today.

Quite aside from the structure of their paired eyes, there are a number of other ophidian peculiarities which seem puzzling when one considers how much alike the habits of snakes and lizards are, but are at once explained by the fossorial-origin hypothesis: it accounts nicely for the loss of not only the limbs but the ears as well, and the parietal eye, dermal color-changes, retinal photomechanical changes,* and some of the same cranial elements which are lacking in the subterranean amphisbænid lizards. All of these things are present in the Varanidæ, and all would certainly have been retained by the snakes if they had originated on the earth's surface.

As the lizard ancestor took more and more strongly to an underground life, its eye probably at first increased in sensitivity. The pupil may even have become a slit, as it is in burrowing boas; and the retina would in any case have lost the oil-droplet pigment, then the droplets themselves, even if the cones were not converted temporarily into rods. The long persistence of the light-shunning habit would permit the degeneration of the whole apparatus of accommodation—and this comprises a good part of the eye: the atrophy of the ciliary muscle made it no longer necessary to maintain a ringwulst, or scleral ossicles, or even scleral cartilage; and of course the ciliary processes were already gone in the diurnal lizard ancestor. As the eye shrank, then, it also became spherical. The spectacle had to be provided early—though as the eye degenerated beneath it, it eventually lost its usefulness for a time. The

*Though this meant only a hastening of a degradation which is seen in all other reptiles as well (see Table II, p. 150).

Harderian gland ballooned, as it has in cæcilians and blind lizards; and—as also in these forms—the lacrimal gland disappeared.

The loss of the fovea and the simplification of the retina involved the optic nerve, which became slender and lost its septa; and the ectodermal conus papillaris vanished along with the need for it. The pupil lost all mobility as the iris muscles disappeared, and the chorioid and sclera coalesced as in rudimentary eyes in general. The canal of Schlemm shrivelled; and the eye finally 'touched bottom' in a condition not much if any better than that of a modern *Typhlops*. Indeed, the organization of the *Typhlops* eye is such that this worm-like form could well have been the 'first' snake (see Plate I).

How long the snakes lived underground, no one can say; but they did not (or did not all) remain there. Coming back to the surface, they were under the necessity of reconstituting their eyes almost 'from scratch'. The vestigial nubbins of visual cells had to be nurtured into bloom as respectable rods. Then, as the race became better able to stand the light, the retina became duplex. The eye enlarged, but in the absence of stiffening structures in the sclera it was forced to remain forever spherical. With the ciliary body and the lens now far out of contact, an entirely novel means of accommodation had to be devised. The remnants of ciliary muscle moved into the iris to play a dual rôle in accommodation and in the operation of the (slit?) pupil.

The recrudescent retina demanded a better nutrition than the thinned chorioid alone could supply. So, the snakes developed a mesodermal conus papillaris, but shortly abandoned this in favor of the more 'direct' vitreal vessels (a change from which the lizards—and the birds—would probably profit if they could make it; see pp. 653-4). They also produced a new 'canal of Schlemm', in a new location and with new connections to the venous system, and elaborated a whole new circulation for the iris (which, if we can go by the cæcilians, probably had no mesoderm left in it during the underground period). And when (in the Colubridæ) the retina finally became pure-cone, with new and unique double elements, supporting a diurnality as thoroughgoing as that of any lizard, the needed yellow filter was manufactured out of the lens itself. With a high ratio of optic nerve fibers to visual cells once more restored, the optic nerve became too plump to remain a simple cord, and an entirely new system of fasciculation and septation was invented for it.

The resulting eye—as we see it today—presents substitutes for all the losses, remedies for all the defects, of the vestigial organ of the

original snakes. And these losses and defects were so numerous that the snakes had almost to invent the vertebrate eye all over again. Nothing like this tremendous feat has occurred in any other vertebrate group, so far as we can tell. No other vertebrates except the placental mammals* have had to do any 'rebuilding' at all. Wherever else the eyes have degenerated, they have remained degenerate as long as their owners survived. We can perhaps understand now why a legless lizard is not a snake simply because it is legless. The snake-shaped lizards such as *Ophisaurus* and *Pygopus* originated above-ground, and escaped the painful period of near-extinction which the true snakes experienced and which they have so gloriously survived.

The Ophidian Retina—Apart from the visual-cell layer, the strata of the modern snake retina are quite orthodox in structure, and it is unlikely that they have undergone any drastic reconstruction as a consequence of the underground babyhood of the Ophidia; for, wherever the eye has become vestigial but has retained a functional retina (*e.g.*, in cæcilians), one notes that though the visual cells are reduced to nuclei each bearing a mere knob of cytoplasm, the nuclear and plexiform layers are still present and distinct.

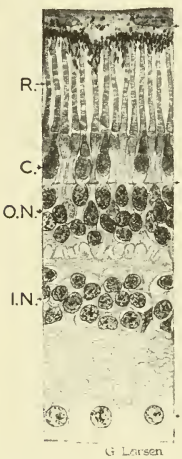


Fig. 184—Retina of one of the Boidæ, *Tropidophis melanurus*. × 500.

P.E.- pigment epithelium; R.- rods; C.- cones; L.- Limitans; O.N.- outer nuclear layer; I.N.- inner nuclear layer; G.- ganglion-cell layer.

The phylogenetic steps between the *Typhlops*-like condition and the mammalian-like retina of the Boidæ are lost, and we can only guess at them (Plate I). The boas and pythons all have the same retina, exemplified in Figure 184 by *Tropidophis,* which has only single cones and rhodopsin-bearing rods. The cones here (as in all snakes) lack not only oil-droplets but also paraboloids and myoid extensibility. In all these respects, they indicate plainly that they were never derived directly from above-ground lizard cones.

Between the Boidæ and the great central family Colubridæ there is again a great gulf, which may be partly filled if ever the retina of

*And perhaps the cod family (see pp. 398-9, and footnotes on pp. 586 and 588).

the osculant *Xenopeltis* comes to histological examination. The 'standard' colubrid retina is pure-cone, with three types of elements, only one of which (Type C) has the structure and staining behavior of the boïd cone; and this type is present only in small numbers at best (Fig. 185a). It was probably the progenitor of the abundant Type A single cone (see Plate I), which in turn somehow gave rise to the unique ophidian double cone (Type B; see Fig. 24, p. 59).

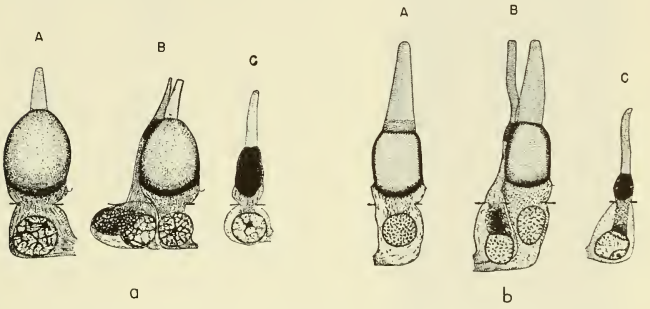


Fig. 185—Representative visual cells of diurnal and secretive colubrids. ×1000.

(Here, and in the illustrations on the next two pages, the homologous elements are labelled with capital letters designating their type; see text).

a, the three cone types present in all diurnal colubrids and elapids (except where Type C has been discarded; see text); drawn from *Natrix natrix*.

b, visual cells of the scarlet snake, *Cemophora coccinea*, exemplifying a number of secretive, crepuscular, and semi-nocturnal colubrids. Note enlargement of the outer segments, and tendency of Type C toward a rod-like form (*cf.* C in Fig. 187).

It is interesting—in fact, fascinating—to note that with their production of this diurnal colubrid arrangement, the snakes had at last struggled back to a pattern which strikingly simulates that of the archaic reptiles: single and double elements which match in structure, plus an 'odd man' in the form of the Type C cone. And, the snakes have wandered off into nocturnality by various pathways, for the Type C cone, like the droplet-free cone of the cotylosaurs and eosuchians, has shown itself to make a better rod than a cone:

In those diurnal colubrids and elapids which exhibit high visual acuity, the Type C cone has been eliminated and types A and B are slenderized

and aggregated (*Malpolon, Dryophis, Sepedon**). In secretive, crepuscular, and some nocturnal colubrids (*e.g., Lampropeltis, Rhinocheilus, Arizona, Cemophora, Trimorphodon*) the outer segments of types A and B are more or less enlarged and tend toward a cylindrical form; but the Type C element is even more rod-like—leads the way, so to say (Fig. 185b). In another assemblage of nocturnal colubrids (*Tarbophis, Dasypeltis, Leptodeira, Dipsadomorphus,* etc.) the Type C element has become a perfect rod and contains rhodopsin, but the other two elements have outer segments which are no more than intermediate between diurnal-colubrid cones and full-fledged rods (Fig. 186). Moreover, the A and B types in these forms are much elongated, as if to put them in the background not only topographically but physiologically. In nocturnal elapids (coral snakes, kraits, etc.), simulations of these various nocturnal colubrid patterns occur, with the Type C element again leading the trend toward secondary rod-hood.

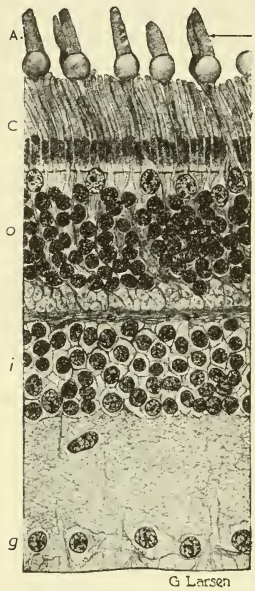


Fig. 186—Retina of *Leptodeira annulata,* exemplifying the *Tarbophis* series of nocturnal colubrids. × 500.

A- single cone (Type A element); B- double cone (Type B element); C, C- layer of rods (Type C elements); *o*- outer nuclear layer; *i*- inner nuclear layer; *g*- ganglion-cell layer.

A very few nocturnal colubrids (*e. g., Hypsiglena, Phyllorhynchus* [and *Lytorhynchus?*]) have converted all three cone types into massive cylindrical elements (Fig. 187†)—perhaps the most spectacular of transmutations, but actually a simple one since these secondary rods lack rhodopsin,

*These forms, when compared with the other members of their families, thus afford an interesting comparison with the lizards: these snakes, and the lizards, have both striven for maximal visual acuity by eliminating the poorest of three cone types—one which makes a good rod, but a somehow poor cone.

†The single and double rods here have no definite mosaic arrangement in the retina, whereas in geckoes the single and double rods form alternate rows running horizontally of the eyeball.

and the retina owes as much of its sensitivity to increased summation as to the lowering of the thresholds of the individual visual cells.

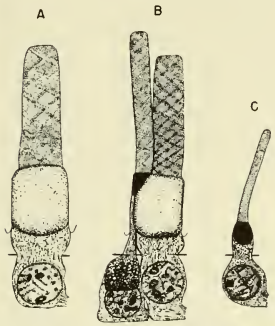


Fig. 187—Representative visual cells (transmuted rods) of a nocturnal colubrid, *Hypsiglena o. ochrorhynchus.* ×1000.

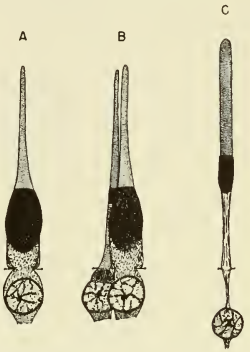
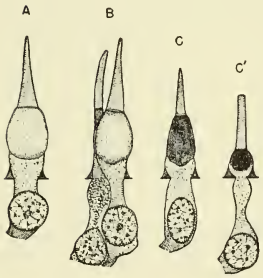
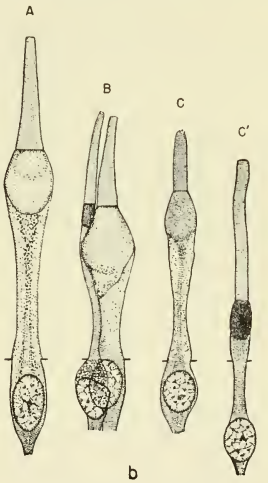


Fig. 188—Visual-cell types in the Crotalidæ: single cone, double cone, and rod; from the copperhead, *Agkistrodon mokasen.* × 1000.



a



b

Fig. 189—Representative visual cells in the Viperidæ (see text). ×1000. a, of Cape viper, *Causus rhombeatus.* b, of puff adder, *Bitis arietans.*

In the vipers (Viperidæ) and pit-vipers (Crotalidæ), derived independently from colubrid ancestors, the diurnal colubrid pure-cone pattern has again been taken over and converted into a duplex one by the transmutation of the Type C cone into a rod. All of the Crotalidæ (moccasins, rattlesnakes, fer-de-lances) show the pattern of Figure 188, with the rods outnumbering the cones about as extensively as in man. The viperid retina is rather more complex. The primitive vipers (*Causus, Atractaspis*) are crepuscular and have nearly-round pupils. The *Causus* retina (Fig. 189a) looks at first glance like a diurnal colubrid one to which a few rods (C′) have been added. The retinæ of the highly specialized vipers (*Cerastes, Bitis, et al*) show the same four types of cells (Fig. 189b); but here the C′ rods outnumber the combined cone types by three to one (in sections). The mystery of the C′ elements clears up when one looks at the retina of the central genus of the family, *Vipera*. In *V. berus* the Type C cones and the Type C′ rods intergrade structurally through an unbroken series of intermediate conditions. *Causus* and *Bitis* have obtained their four types of visual cells simply by getting rid of the intermediates between two of them, which *Vipera*—fortunately for the comparative retinologist—has never eliminated.

Two colubrid genera, *Farancia* and *Abastor,* resemble *Vipera* closely; but this is of course no implication that the Viperidæ stemmed from such colubrids, any more than the essential similarity of the crotalid and *Leptodeira* patterns implies a genetic relationship.

The plasticity of the ophidian retina is thus enormous. The snakes alone have rung as many changes upon their visual-cell patterns as have all the other vertebrates put together (Plate I). If anything could make a snake-hater learn respect and admiration for this abused group of animals, it would be the study of their eyes. The writer speaks from personal experience!

Chapter 17
BIRDS

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The avian eye contains no feature of any importance which does not also occur in some reptilian group, and practically all of its features occur in the lizards—not because the birds came from lizards (their ancestors were certain of the dinosaurs), but because nothing material has needed to be changed, in the eye, during the descent of the lizards and birds from their immensely remote common ancestors, the eosuchians.

Though the birds comprise a whole vertebrate class, containing thousands of species divided among many orders, the eye is as uniform throughout the group as it is in any one order or suborder of reptiles or amphibians.

The Eye as a Whole—The great size of the bird eyeball—the primary basis of the paramount eye-mindedness of the group—goes unrealized by the casual observer, for only the relatively small cornea shows in the circular lid-opening. Only the tiniest of birds, such as hummingbirds, warblers, and finches, have eyes as small (6-8mm.) as those of the aver-

age amphibian or reptile. The two eyes of a bird often outweigh its brain, and there is often barely room enough for them in the head. The largest land-vertebrate eye is that of the ostrich, 50mm. in diameter. Hawks and owls, a fraction of the size of a man, have eyeballs as large as ours and larger.

Such eyeballs are necessarily a tight fit for their orbits. There is no room for a muscle cone like that of a shark or a man. The reptilian retractor bulbi muscle has been discarded—leaving behind it, however, its derivative, the bursalis (see Figs. 142b, 143c and f; pp. 420-1). The oculorotatory muscles are ribbon-like, and plastered snugly against the globe (Figs. 70, 107d; pp. 172, 270). They never extend forward beyond the limits of the convex posterior portion of the eye; hence, where the latter is tubular (Fig. 190c), the muscles are relatively short (and, in owls and some eagles, functionless).

The shapes of avian eyes fall into three rough categories: flat, globose, and tubular (Fig. 190). In all, however, there is a prominent concave region which coincides with the zone occupied by the ciliary body and the ring of scleral ossicles which creates and supports the concavity. In the 'flat' eyes exhibited by a very great majority of birds, the axis is much the shortest of the three diameters, equalling but seven- or eight-tenths of the vertical. The shape of these eyes is thus the same as in the lizards. In those diurnal birds which need high resolution at great distances (*i.e.*, wing-feeding insectivorous forms, predators in general, and such types as the crow), the ratio goes as high as unity, yielding the 'globose' form of eyeball. In most owls (and some eagles) the axis is as long as the other diameters or even a bit longer, and at the same time the concave zone is so broad that the eye is rendered 'tubular'. In these instances the retinal area is relatively small; but the retinal *image* may be either small (where the lens is closer to the retina and rotund—owls) or large (where the lens is farther forward and flatter—eagles). Accompanying the increase in relative axial length one sees invariably a proportionate broadening of the curvature of the posterior segment, so that the junction of this region with the concave zone becomes more and more conspicuous. Except where the lens recedes into the eye and sharpens its curvature (as in owls, *Podargus,* etc.), the phylogenetic increase in the axial length of the bird eye can always be described as adaptive toward the securing of higher visual acuity, through an increased 'throw' of the image from optical center to retina and the consequent broadening of the image at the visual-cell level.

Horizontal ellipsoidality is slight at most—the ratio of the horizontal diameter to the vertical is usually 1:1 and never greater than 1.2:1. But nasad asymmetry is universal: the cornea and lens are not only tilted toward the beak, but shifted in that direction as well (Fig. 190; Fig. 71, p. 173). This effort to secure a maximal overlapping of the monocular visual fields is just as great, or greater, in elongated eyes whose retinæ and visual fields are restricted by their tubularity.

The sclera always contains a hyaline-cartilage cup, which extends forward to the back edge of the ossicular ring, where it is usually locally

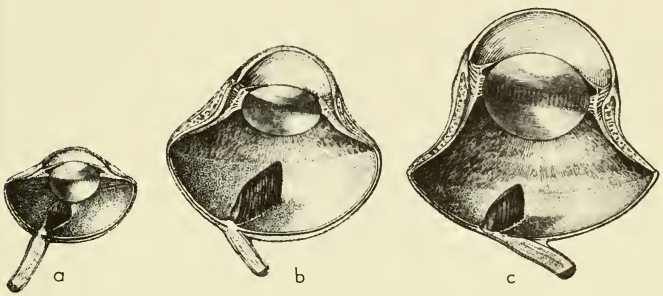

Fig. 190—Bird eyes, showing characteristic shapes. ×1. After Soemmering.

(Each drawing shows the ventral half of the left eyeball; the nasal side is to the right; the plane of the ora terminalis retinæ has been placed horizontally to bring out the nasad asymmetry which is present to some degree in the eyes of all birds).

a, commonest, 'flat' type (in a swan, *Cygnus olor*). b, 'globose' type (in an eagle, *Aquila chrysaëtos*). c, 'tubular' type (in an owl, *Bubo bubo*).

thickened. External to the cartilage is a dense fibrous layer, often as thick as (or thicker than) the cartilage itself, particularly in the fundus and particularly in large eyes. Surrounding the optic nerve there is often (most often in small eyes*) a plate of bone, the 'Gemminger's ossicle'. This may be horseshoe- or washer-shaped, or may be represented by several separate pieces. It is set in the cartilaginous cup as if formed from a portion of the latter's substance; but its mode of development is unknown, as is also its physiological value. The anterior scleral ossicles

*And supposed to be conspicuously developed in the woodpeckers; but it is lacking in the flicker.

(Fig. 107, p. 270) overlap the scleral cartilage externally (Fig. 191), and extend forward nearly to the limbus. Their number ranges from ten to eighteen, except for rare instances among diving birds, where the basic number has been increased by anterior and posterior fragmentation. Fifteen is the commonest number and perhaps the 'original' one. In a summary of 460 species of birds, Lemmrich found the ossicle numbers to be distributed as follows:

No. of ossicles:	10	11	12	13	14	15	16	17	18
No. of species:	1	18	26	57	138	182	31	3	4

Though the ossicle of Gemminger, despite its thinness, usually or always contains marrow spaces, such are present in the anterior ossicles only where these are largest and thickest (owls, frogmouths, hawks, eagles, etc.). The fact that the bony ring is made up of separate pieces probably has no physiological significance, but Lemmrich has pointed out that the ring could not otherwise grow with the eyeball.

The cornea is usually relatively small in area, and especially so in underwater swimmers; but it becomes larger in globose eyes and very large and strongly arched in nocturnal forms. It is ordinarily somewhat thinner at its apex than at the periphery, but in large eyes the thickness of the cornea tends toward uniformity everywhere. In spite of its customary eccentric position, it is almost always circular in outline and neatly fills the lid opening. Histologically, the avian cornea is quite like that of man, though a Bowman's membrane is not always differentiated.

The corneal surface is kept especially well polished by the action of the nictitating membrane with its lining of papillose cells. The nictitans also cleans off the inner surfaces of the other lids, and keeps them from smearing the cornea, in those birds in which the lids close just after the nictitans in a 'blink' (*e.g.*, pigeon). The nictitans has a marginal pleat which slides easily under the lids in the 'going' direction, but scrapes them on its way back. In many birds or most, the lids close only in sleep and the nictitans alone blinks. In consequence, the upper and lower lids have a largely unstriated, slow-acting musculature.*

The chorioid is relatively thick—more so than in mammals and much thicker than in reptiles. It is thickest in the fundus. Its distinct vessels appear to be mostly arteries, and these lie close to the choriocapillaris which they supply. Between them and the thin, pigmented 'lamina fusca' (applied loosely to the sclera) lies a thick region which in prepared slides

*In altricial birds the lids are closed for a time after hatching, but in all birds they are wide open before hatching, not fused edge-to-edge as in fetal mammals.

appears largely empty, but actually has a sinusoidal (lymph? venous?) structure. Traversing this thick open layer, with their direction radial with respect to the eyeball, there are connective-tissue cords and columns which often contain (or consist largely of) muscle cells. These may be

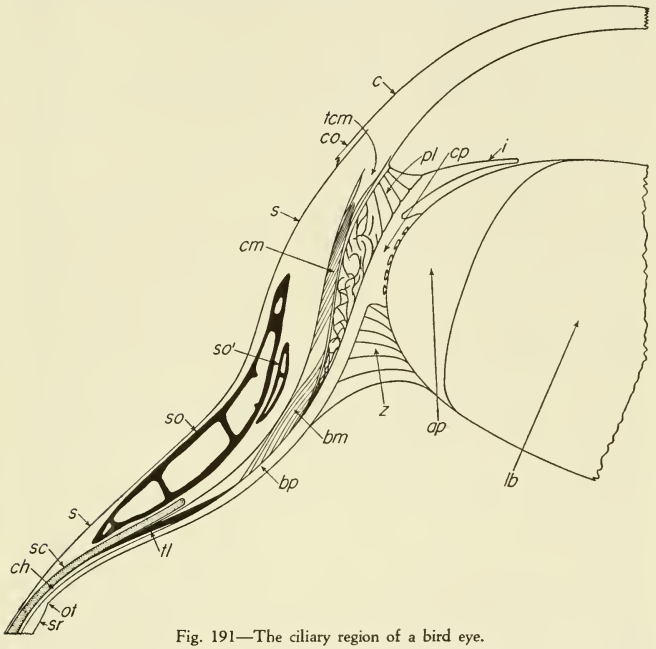

Fig. 191—The ciliary region of a bird eye.

(Semi-diagram of the temporal quadrant in the red-tailed hawk, *Buteo b. borealis*. Blood vessels, including the canal of Schlemm, omitted).

ap- annular pad or ringwulst of lens; *bp*- base-plate of ciliary body; *c*- cornea; *ch*- chorioid; *cm*- Crampton's muscle; *co*- conjunctiva; *cp*- ciliary process; *i*- iris; *lb*- lens body; *ot*- ora terminalis; *pl*- pectinate ligament; *s, s*- sclera; *sc*- scleral cartilage; *so*- scleral ossicle; *so'*- overlapped portion of adjacent scleral ossicle; *sr*- sensory retina; *tcm*- tendon of Crampton's muscle; *tl*- tenacular ligament; *z*- zonule.

smooth or striated, and their contraction would obviously thin the chorioid temporarily and draw the retina backward. In the flicker (and other woodpeckers?) the chorioid is not empty-looking, but contains a thick mass of mucoid tissue which has probably been developed to prevent

a repeated forward movement, and detachment, of the retina during 'wood-pecking'. The chorioid in most birds is highly ductile in the direction of its thickness, *i.e.* radially of the globe: Abelsdorff and Wessely found that if the anterior chamber of a bird is drained by corneal punctures, the chorioid will promptly thicken enormously through engorgement.

The avian chorioid is not known ever to contain a tapetum lucidum, though some old accounts, not since substantiated, mention one for certain owls. The eyeshine of the goatsuckers (nighthawks, whip-poor-wills, etc.) is so vivid however that the eyes of these birds, for this and other reasons, seem most attractive objects for study.

Anteriorly, the chorioid thins out and becomes the base-plate of the ciliary body (Fig. 191), which angles sharply inward toward the axis and leaves a large space between itself and the sclera, to be traversed by the many strands of the pectinate ligament. The ciliary processes occupy the whole ciliary zone (so that there is no true orbiculus), and are very numerous—sometimes numbering in the hundreds, though only a majority are tall enough to reach the lens capsule and fuse therewith. The number of processes goes roughly with the size of the eye, and from eye to eye they do not vary greatly in thickness. From the ciliary processes, and from between them, there originate the fibrils of the zonule, the anteriormost of which are squeezed between the iris and the ringwulst, as in lizards.

The ciliary muscles, as in lizards, are more closely associated with the sclera than with the uvea. They may be arranged as in Figure 191 or, probably much more commonly, the muscle of Brücke originates from the *inner* side of the thin scleral sheet which forms the anchorage of the pectinate ligament and covers the inner side of Crampton's muscle. Brücke's muscle is sometimes divided into an anterior and a posterior portion; then, the anterior is properly known as 'Müller's muscle'—first described by Müller in the goshawk, *Accipiter gentilis*. Other variations are mentioned on pp. 279-81 and 439-42.

The 'canal of Schlemm' is complex, represented not by a single venous annulus, but by two, with moreover an associated artery which lies between them (in *Passer domesticus,* two arteries), and has a likewise annular course. The connections and relationship of the veins and artery(s) are not yet known. The whole complex lies near the limbus, attached by connective tissue to the inner surface of the sclera near the anterior end of Crampton's muscle.

The iris is often extremely thin just at its root, where the anteriormost pectinate-ligament fibers attach, like a zonule of the iris. Here the iris may be reduced to little more than the retinal layers.* It promptly thickens greatly, then slowly tapers toward the pupil margin where it often has a knife edge (in contrast to the lizards; but *cf. Sphenodon*). Sphincter and dilatator fibers, all striated, are distributed throughout the width of the iris. These originate embryologically from the anterior retinal layer at the pupil margin. Their action, like that of the avian ciliary muscles, is extremely rapid. Both retinal layers of the iris are pigmented; but a second dilatator system, identical in genesis with the dilatator of mammals (and with its elements probably unstriated and perhaps syncitial), has been described by so many investigators that its existence in at least some birds cannot be categorically denied. The circulatory pattern of the iris is much as in lizards, with a wide plexus of capillaries supplying the sphincter and drained peripherally by short radial veins. Small vessels are concentrated near and at the anterior surface of the iris, from which many of them protrude (as in many reptiles and amphibians). Here also is concentrated the stromal pigmentation, which may incorporate many types of cells—particularly lipophores. There is no unbroken layer of mesothelium on the face of the iris. Though it literally squeezes the lens only in certain amphibious birds, the avian iris is always of material assistance during accommodation, in holding back the lens against which it presses, and in inhibiting the peripheral part of the anterior surface of the lens from bulging, thus concentrating the change-of-curvature in the part of the surface opposite the pupil.

The lens is as highly refractive as in mammals, often more so, though it is often very soft, particularly where the range of accommodation is great. As in most of the higher vertebrates, the anterior surface is less sharply curved than the posterior. It is flattest in most diurnal birds (index 2.2-3.0), roundest in crepuscular and nocturnal forms, and in divers (1.2-1.85). The annular pad or ringwulst is ordinarily well developed, and as a maximum (in *Apus*) it may take up half the area of a sagittal section of the whole lens. In general, its relative thickness goes with the capacity for accommodation, but it is very thin in diving birds (loons, murres, cormorants, etc.), particularly in those whose iris sphinc-

*In captive owls which have been roughly handled, one sometimes sees an irregular second pupil at the periphery of the iris, held open by the tonus of the sphincter. Such a defect is not a 'coloboma', of embryonic origin, but has been produced by a local traumatic rupture of the iris root, which is especially delicate in these birds.

ters do more of the labor of accommodation than their ciliary apparati. The ringwulst is small also in flightless birds (*Apteryx,* ostriches) and smallest of all—practically non-existent—in the Australian terrestrial goose *Cereopsis.*

Between the ringwulst and the lens-body there is a slender space, a vestige of the cavity of the embryonic lens vesicle (see Fig. 40e and f, p. 110), into which the inner ends of the ringwulst fibers secrete a fluid substance. This perhaps serves only to lubricate the interface between the ringwulst and the lens proper as the two shift past each other during the accommodatory deformation of the lens. But it has been suggested that there may be enough of the fluid to make a sharply-curved blister under the anterior lens epithelium, when the fluid is squeezed forward by the pressure of the ciliary processes. A 'bump' does form on the anterior face of the accommodating lens, but this may be wholly due to the mechanics of the lens and ringwulst and the orientations of their respective fibers, and to the restraining pressure of the iris (*v. s.*) That the sphincter contracts (stiffening the iris) during accommodation is indicated by the tautening of the pectinate ligament, demonstrated beautifully by Wychgram (and see Fig. 109, p. 275).

The Pecten, and Its Analogues in Other Vertebrates—The most conspicuous and perennially interesting feature of the avian eye is its pecten (Fig. 192; see also Figs. 80 and 114, pp. 188, 308). The pecten projects into the vitreous in the ventral half of the eye from the head of the optic nerve, with which its base roughly coincides. It consists largely of small blood vessels (of greater than capillary size). If these be considered comparable to the vascular supply of organs in general, then the pecten must be described as an essentially ectodermal papilla, for its scant framework is composed of neuroglial cells of optic-cup origin. It is always pigmented (though occasionally only lightly), with the pigmentation progressively deepening toward the apex of the structure and heaviest of all in the 'bridge' which ordinarily binds and caps its free end. The vascular supply of the pecten has no connection with that of the chorioid, but its chief veins and arteries are probably homologous with those which supply the falciform process, hyaloid or vitreal vessels, conus papillaris, and retinal vessels of fishes, amphibians, reptiles, and mammals.

Two types of well-developed pectens occur; their morphological and genetic inter-relationships are obscure. The palæognathous birds, which are primitive and (except the tinamous) flightless, characteristically have

a pecten exemplified by that of the ostrich, *Struthio camelus* (Fig. 192a). Here the organ has a central vertical panel which is buttressed along its sides and ends by lateral vanes (Fig. 192c). The same plan is followed by the 'American ostrich' (*Rhea*) and apparently by the tinamous. The situation in the emu (*Dromæus*) is unknown; but in the

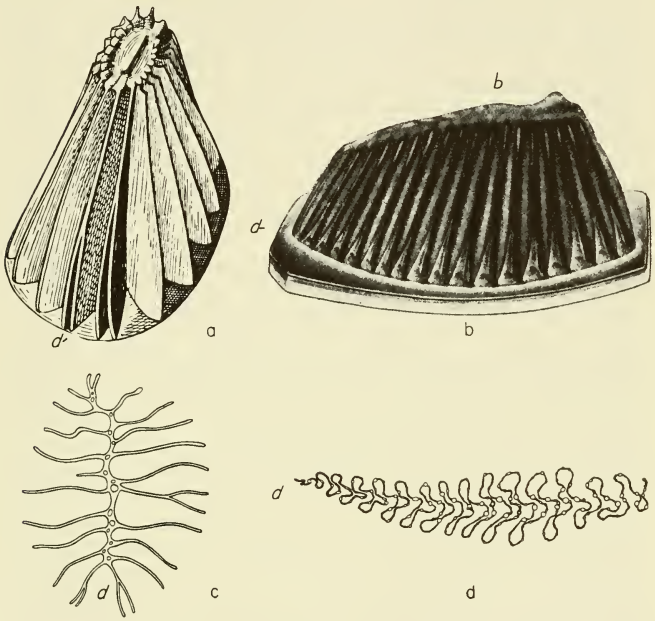

Fig. 192—The pecten.

a, pecten and optic disc of ostrich, *Struthio camelus*. ×5. After Franz.

b, portion of eyeball wall bearing pecten of domestic fowl, exemplifying type present in most birds. ×8. After von Szily.

c, section of a near, and parallel to, its base, showing central web and lateral vanes. After Franz.

d, section parallel to base of pecten of red-tailed hawk, *Buteo b. borealis*, showing pleated structure characteristic of the common type of pecten shown at b. ×7.

b- 'bridge' which cements folds distally; *d*- dorsal end of pecten.

cassowaries (*Casuarius* spp.) the pecten is built as in the neognathous birds:

The Neognathæ* all have the pecten organized as an undulant or accordion-pleated fin, superficially resembling an ordinary steam-heating radiator (Fig. 192b, d). The pleats of such a pecten, when it has been excised, can be smoothed out and the whole organ rendered plane, but only after the apical bridge has first been cut away. The basal area of the organ, the extent to which its ventral end is free of the nerve head, the number of its folds, and the closeness of its approach to the ventral ciliary body and to the ventral periphery of the lens, are all subject to great variation. Its location is constant, however—in all birds the long axis of the base of the structure is directed along the former course of the embryonic fissure of the optic cup; for, since its glial framework develops from the head of the optic nerve, it necessarily conforms to the fissure as does the elongated head of the nerve itself.

One of the flightless genera of palæognaths, that of the kiwis (*Apteryx*), has a pecten which is really a conus papillaris, identical with that of many a lizard (see Fig. 182, p. 632). The eyeball of this large nocturnal bird is only 8.0mm. in diameter and in axial length. The slim pecten is reported to be 2.0mm. tall and 0.3mm in diameter along its shaft; there are no vanes or pleats. It would be natural to suppose that the kiwi pecten is primitive, and links the vaned and pleated pectens with the simple ancestral reptilian conus papillaris. Such an interpretation is denied us: the kiwi eye—including its pecten—is as degenerate as it is possible for an avian eye to be. It is myopic and affords its owner only very poor vision both by night and by day; and it is tiny, whereas the orbit is huge—implying that the eye has dwindled greatly in size. According to Kajikawa, the eye accomplishes no growth whatever between the 'hen-sized' juvenile condition and the 'turkey-sized' adult stage.† The kiwi, unlike all other birds, appears to have a good sense of smell—so good, indeed, that it is the guiding sense, instead of vision.

A great many surmises have been made as to the function of the pecten, the first of them not many years after its discovery in 1676. Nearly all its students agree that it must nourish the interior of the eye; but its peculiar form, and particularly the great variations in its form

*This superorder includes all living birds excepting the ostrich-like forms and tinamous (superorder Palæognathæ) and the likewise primitive penguins (superorder Impennes).

†For comparison, note the eye of a turkey, shown at natural size in Figure 142a and b, p. 420.

and size, have made it seem unlikely, to most, that nutrition is its chief purpose. So, a great deal of thought has been spent upon its interpretation. One of the most recent and interesting theories has been discussed on pp. 365-7. It has been variously held to cast a shadow on the retina, or not to do so; and the supposed shadow has been involved by one investigator in movement-perception, and by others in the prevention of monocular diplopia during binocular vision, or in the suppression of the binocular field during monocular fixation. It has even been considered to serve as a 'dark mirror', transforming a too-bright image (cast upon it by the lens) into a comfortably-bright one (relayed from it to the retina), and making it possible for a ground-feeding bird to see an approaching hawk in the sky without looking upward. The pecten has been believed to adjust intra-ocular pressure (by swelling and shrinking) during accommodation or during changes in the altitude of flight, to serve as a proprioceptive sense-organ for the regulation of accommodation, or even to assist mechanically or hydraulically in the deformation or displacement of the lens. It has been held to be primarily a heat-radiator, of especially great value to arctic, alpine, and high-flying birds. To it has been ascribed a function similar to that of the holostean-teleostean chorioid 'gland'—the smoothing out of intra-ocular blood-pulsations, analogous to the action of an air-chamber on a reciprocating pump.

To each of these theories so many objections stand in the literature that we shall not consider them in detail here. Suffice it to say that it is unlikely that the pecten casts a shadow outside of its own base—or casts one where it would do any good; that its shape, volume, and position have not been found to alter during accommodation; that its size does not correlate with the coldness of the air to which its owner exposes itself; that it could not conceivably reflect an image even as good as those one sees in fun-house mirrors; and that no sensory nerve fibers or endings have ever been demonstrated in it. We can cling, however, to the demonstrations by Abelsdorff and Wessely of a ready diffusibility of blood solutes through the walls of its vessels (despite their peculiar and thick hyaline coats) into the vitreous, and of its capacity for compensatory hypertrophy following the surgical excision of the ciliary processes.

It is because the writer does not believe that the pecten has any 'ulterior' function—particularly, any function with a directive connection with the relationship of the eye to the environment—that the struc-

ture has found no great place in the ecological Part of this book. We shall find reason to consider the pecten related to the habits, particularly the visual habits, of birds; but it is the habits which have molded the pecten, not the pecten which brings about the habits. To obtain a proper perspective on the intriguing variations of the pecten, it will be necessary to make an apparent digression and consider the whole comparative picture of which the pecten is but one detail:

In the first place, it must be borne in mind that the only fast-living tissue in the whole posterior segment of the vertebrate eye is the sensory retina. The one richly vascular structure universally present is the chorioid coat; but all the blood-filled tubing of the chorioid exists simply in order to maintain a rich flow in the choriocapillaris; and the latter exists solely to nourish the retina—with special reference to the greedy rod-and-cone layer. If the requirements of the visual cells are not too high, there may be enough pabulum left in the trans-retinal exudate of the choriocapillaris to care adequately for the needs of the inner layers of the retina. We should expect this to be the case, *ceteris paribus,* when the rods are abundant and the more highly metabolic cones are absent or present only in reasonable numbers. But if the chorioid of a particular eye cannot supply a cone-rich visual-cell population in an extensive retina, *and* the neuronic layers of that retina as well, then we may expect to find some additional vascular device, advantageously situated to supply the inner reaches of the retinal tissue. Ciliary processes, when present, are not so situated; for they lie too far anterior to the main mass of the retina, and their secretion (the aqueous humor) passes too largely and directly into the anterior chamber and is too promptly drained therefrom.

We found no supplemental nutritive device (hereinafter to be abbreviated as 'S N D') in the lampreys. These forms have small eyes, but most have many cones and tend toward diurnality. Their eyes are perhaps simply too primitive to have achieved physiological perfection.

The absence of any S N D in the elasmobranchs is readily understood in view of their nocturnality and their pure-rod retinæ.* Nor should the modern chondrosteans require anything more than their chorioids. In the holosteans and teleosts, however, we have essentially arhythmic and bright-light groups, and we note that these fishes are all provided either

* Mere habitual exposure, as such, to strong light—apart from an accompanying high cone:rod ratio—may tend to demand an S N D; it does not seem to have occurred to physiologists that a bright, minified image will inevitably warm the retina and quicken its metabolism.

with a network* of 'hyaloid' vessels at the vireo-retinal interface, or with a falciform process—an obvious physiological counterpart of the avian pecten (the pecten being essentially an ectodermal imitation of the older structure!). It is not too much to hope that someone will sometime determine whether the retinæ of the hyaloid-vessel teleosts have greater requirements of glucose and oxygen than those of the falciform-process species. The retention of one S N D or the other in even the most strongly nocturnal teleosts may seem disturbing to our thesis; but their nocturnalities are probably all secondary, and there has been no such urgent need to eliminate an S N D from a secondarily nocturnal eye as to evolve one in a secondarily diurnal one. The presence of vitreal vessels in *Polypterus, Protopterus,* and *Lepidosiren* may have such an explanation.

Among the anuran amphibians, the ranid frogs alone exhibit the primitive arhythmic or diurnal habit of the group, as is evidenced by the persistence of yellow cone oil-droplets in those forms alone. All known anurans have vitreal vessels, whose presence (in as full development?) in the secondarily nocturnal toads and tree-frogs is thus a failure-to-discard. It is only natural that the urodeles and cæcilians have never developed such vessels.

Turning to the reptiles, we are confronted by the paradox that neither the diurnal turtles nor the nocturnal crocodilians have preserved the ancestral conus papillaris in a useful condition. Its loss in the crocodilians (and in *Sphenodon*) makes good sense; but the turtles all have many cones—some, perhaps, only cones—in their retinæ. The turtle rates as 'sluggish' alongside the average lizard. The latter has the conus, of course; and it would be interesting to know whether the requirements of the relatively crude (though cone-rich) turtle retina are sufficiently lower than those of lizard retinæ to explain the difference with regard to the conus. Again, among the lizards themselves, the relative size of the conus does not go perfectly with diurnality-versus-nocturnality: it is smallest in certain geckoes and other nocturnal lizards (*Pygopus,* etc.); but there are geckoes with large coni, and the chameleons have very small ones. Anyone who has ever watched the 'slow-motion' performance of a true chameleon, however, should be willing to imagine that its retinal metabolism may be little if any higher than that of a tortoise. As for the geckoes, there are reasons for thinking that their peculiarly pure-rod retinæ have a physiology much like that of a pure-cone one.

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*Richer in *Lepisosteus* than in *Amia,* according to Virchow.

In the snakes, we have a pretty analogy for the situation in the teleosts, for here a mesodermal vascular papilla has been given a trial, and practically abandoned in favor of a vitreal-vessel system (the latter presumably more efficient, since it is in so immediate contact with the tissue which it serves). The retinal plexus does not seem to have reached a high state of development in the Boidæ (which are nocturnal), but it has full expression in the Colubridæ, where the total area of its vessels is said to equal one-third of the whole area of the retina; and it has persisted unchanged in the higher families despite their wholesale reversions to nocturnality—perhaps because the ophidian chorioid had become so very thin, so that it was as easy to keep the hyaloid vessels as to discard them and rebuild the chorioid (*cf. Protopterus!*).

To anticipate the next Chapter: the mammals characteristically have many vessels and capillaries embedded *in* the inner layers of the retina. This greater intimacy of relationship, as compared with the fish-anuran-snake situation, is only to be expected since the mammals are warm-blooded and those other groups are not. Just so, the buttressing or pleating of the avian pecten (often claimed to promote structural rigidity, which of course it incidentally does) is a secretory-surface-increasing device which these hot-blooded creatures require, in contrast to the lizards and the extinct reptiles which really evolved the lizard conus. A vestigial conus occurs in many of the lower mammals, particularly in marsupials and rodents. The retinal vessels are lacking in the monotremes, and are lacking or greatly reduced in many other nocturnal mammals. They are best developed in the (diurnal) primates and in the (arhythmic) ungulates and carnivores. Where, as occasionally, the retinal vessels extend out to the outer nuclear layer as if to supply even the visual cells themselves, it is in forms whose chorioids are exceptionally under-developed (dormice, flying-squirrels) or are insulated from the visual cells by a relatively impermeable retinal tapetum (opossum; the retinal tapetum of the crocodilians also seems to interfere, for the chorioid is extra-thick behind it—p. 613). It is a toss-up whether the embedded retinal-vessel system of mammals, or the pecten of the birds, is 'better'. The retinal vessels are a more direct means of supplying the retina; but the pecten perhaps interferes less with vision—the mammalian retinal vessels have always to be excluded from the vicinity of a fovea.

The whole S N D picture thus reveals a rather consistent relationship with habits which would seem to carry with them a high level of retinal

metabolism, such that the chorioid is unable to take care of the whole thickness of the retina—occasionally, unable to supply even the whole requirement of the visual cells alone. We can now again approach the avian pecten, prepared to inquire more astutely whether its variations really demand explanation other than the one which seems to cover the supplemental nutritional structures of other vertebrates.

A large amount of information on the size of the pecten in different birds has been gathered together by Kajikawa and Franz. It is not easy to interpret the data, for as often as not only the number of folds of the pecten has been recorded. This value is however as useful as any other single one; for even if we knew the length, width, and height of a pecten, and its total surface area, we should still need to know its total blood-vessel area, blood capacity and rate of flow, the area and volume of the retina and its rate of oxygen- and glucose-consumption, before we could compute any very precise ratios as a basis for the comparison of one eye with another. Not all of these facts are known for any one bird, let alone for an assortment of birds with various habits.

In a great majority of birds, the length of the base of the pecten is about equal to half the horizontal diameter of the eye, and the number of folds in the pecten runs high—about 14-27, with 30 as the maximum (in *Garrulus glandarius*). In this category are most of the ground-feeding, gallinaceous birds and the perching birds (Order Passeriformes, comprising about half of the 20-odd thousands of kinds of birds). These, and indeed most other birds, feed upon small objects and have high capacity for resolution and accommodation in proportion to the size of their eyes. Still greater ranges of accommodation are found in the largest-eyed predaceous birds, the hawks and eagles. In these birds the volume occupied by the pecten is relatively about as large as in most passerines, but the folds are coarser and consequently somewhat fewer (mostly 13-17). The owls and swifts are known to accommodate but little. Owls have only 5-8 pecten folds, and the number in *Apus apus* (11) is just low enough to call 'low'.

These generalizations have been known for some years, and have led many investigators to agree with a theory of Rabl, which he based upon correlations of the number of pecten folds with the relative size of the ringwulst (which, as we have seen, is essentially involved in sauropsidan accommodation). Rabl held that since the degree of development of the pecten goes with the degree of development of the accommodatory mechanism, the pecten must be a part of that mechanism.

This correlation with accommodation still stands despite all the evidence, experimental and otherwise, that the pecten has nothing to do with accommodation. If the relation of the two is not causal, then we must look for a third correlate which ties the first two together. This appears to be furnished by the retinal metabolic rates of the birds:

If, as the comparative S N D situation suggests, the retinæ in actively diurnal vertebrates, with relatively high visual acuities, consequent high cone:rod ratios, and good accommodation, have higher metabolic requirements than the rod-rich retinæ of nocturnal, crude-visioned, poorly- or non-accommodating forms, then of course we should expect the avian pecten to 'go with' accommodation; but it is really going with diurnality, high visual acuity, and bustling activity.

Reviewed with this thesis in mind, most birds do seem to have either large and many-folded pectens, or small ones, depending upon their behavior toward illumination and their general level of activity. In nocturnal birds, the length of the base of the pecten is decidedly *less* than half the eyeball diameter. Among the palæognaths* the ostrich and rhea are bold, light-loving creatures and have up to 25 or 30 pecten vanes. The cassowary is shy and crepuscular, spending most of its time in the densest forests, and has a small pecten with only 4-5 folds. Moreover, the cassowary pecten appears degenerate in that it has been invaded by mesodermal connective tissue. The lizard-like pecten of the strongly nocturnal *Apteryx* has no vanes at all, whereas those of some lizards have three or four.

It has been shown that the pecten of a large owl (*Bubo bubo*) is smaller than that of an eagle (*Aquila chrysaëtos*) having the same retinal area. Smaller owls compare in this same way with hawks; and the pecten in all owls is incomplete in that it lacks a 'bridge'. The nocturnal frogmouths (*Podargus* spp.), close relatives of the owls, have bridgeless pectens which are relatively even smaller, with but three or four folds. The European goatsucker *Caprimulgus europæus*, another nocturnal owl-relative, has three to five pecten folds.

Among ducks and geese, which mostly have 10-16 folds, a conspicuous form with its six folds is the peculiar *Cereopsis*, a goose which seldom leaves the ground (and, incidentally, has practically no ring-wulst). The nightingale, *Luscinia megarhyncha*, has been claimed to have only five folds; but this is an old and doubtful record. The parrots

*Whose radiate pectens should probably be considered separately until we know more about their relationship to the undulant pectens of other birds.

have rather low fold numbers—7-14. This is hard to explain away, for most parrots are active diurnal birds and fly a good deal. They would seem not to have high visual-acuity requirements, however; for, with the exception of the notorious sheep-killing (?) kea, they restrict themselves more to gross vegetable food than do any other birds. The eyes of parrots bear other surprises, and would be well worth intensive study: they have the narrowest known binocular fields (p. 295), and lack the customary red oil-droplets (pp. 499-500). It can be said, though, that *within* the parrot group the number of pecten folds varies as one might expect, for the nocturnal owl-parrot (*Strigops habroptilus*) has only four to six folds.

Rather low numbers (*i.e.*, less than 12) occur in many sea-birds, shore-birds, herons etc. Some of these are nocturnal, others not. One clear-cut example of correlation—which could be multiplied—is the stone-curlew (*Burhinus œdicnemus*), which feeds only at night, has very large eyes, and has only eight pecten folds.

The general correlation of large, elaborate pectens with diurnality and of reduced folds with nocturnality was noticed by Wagner back in 1837. This was thirty years before the formulation of the Duplicity Theory; and it was only long after 1867 that it was first realized that cones and rods might have very different metabolic rates and requirements. Wagner studied 108 species of birds, and though all the additional species examined since have only borne him out, his idea has been quite ignored or forgotten since the turn of the century when Virchow last accorded it a few words in print. Jokl did not know of it when, in 1923, he perceived the physiological interchangeability of the various S N D's—but thought that the metabolic level of a retina, determining the need or dispensability of an S N D, was governed by the activeness of the animal. Thus, he explained the absence of a conus in both turtles and crocodilians on the basis of sluggishness (forgetting *Sphenodon,* which also lacks a conus and is sluggish as well as nocturnal), and he accounted for the reduced pectens of *Apteryx, Casuarius,* and *Struthio* (*sic*) on analogous grounds—*i.e.* flightlessness. The ostrich has plenty of 'folds'; and, though flightless, it is very far from sluggish.

Wagner and Jokl were each on one rail of the right track. From all present indications it does not appear that we need ascribe to the pecten any 'intentional' activity other than the giving off of nutrients for the retina to absorb from the vitreous. That it gives off heat (which however is not needed) goes without saying. That considerable water escapes from it also is clear from certain of Abelsdorff and Wessely's experi-

ments; but this serves only to provide water which, in a pectenless eye, the vitreous would get from the ciliary epithelium anyway. The need for a pecten (or for any other S N D), and for a large one or a small, seems to depend solely upon the rate-of-living of the sensory retina. Some of the factors, at least, which heighten this rate are diurnality, activity, and high retinal temperature (owed chiefly to warm-bloodedness, but assisted by the absorption of photopic images in the contiguous pigments). Conversely, it is depressed by the elimination of cones in nocturnality, by sluggishness, and by low retinal temperature.

The interplay of these factors is various. Probably the turtle, though diurnal, needs no conus because it is sluggish. Probably the large geckoes, though nocturnal, need one because they are extraordinarily active. Probably the chameleon's conus is tiny because the animal, though diurnal, is sloth-like in all its movements except the extension of its fly-catching tongue. Probably the flying-squirrel, though nocturnal, needs retinal capillaries because it is active and warm-blooded. But these are guesses—we have no cold figures on the retinal metabolism of these forms, and of their close relatives which have different habits and different S N D conditions.

Before any final ballot is taken on the prosaic theory offered here in explanation of the S N D, in general, and the many more glamorous and intrinsically more 'attractive' interpretations of the pecten, we need very badly to know more about the *true* sizes of pectens—the area over which they expose the blood circulating in them, the rate at which the blood is changed for fresh, the permeability of their vessels, and so on. Then, such data must be compounded with the status of the chorioid, with the area, thickness, and histology of the retina, and with the results of *in vitro* determinations of the metabolism of unit pieces of retinal tissue from various birds and various other vertebrates, wisely selected in the light of the whole S N D situation.

These are problems for a physiologist to attack: he has the apparatus and the methods*; and he can be assured in advance that his findings will be of great value in themselves even if they do not yield correlations which take the mystery out of the pecten. To date, ornithologists and ophthalmologists have been too content to sit back and speculate about the pecten, though they were told by von Husen, back in 1913, that only physiological experimentation would reveal the whole meaning of the structure. As Mark Twain said of the weather, everyone talks about the

*See, for example, the paper of Lindeman (1940).

pecten but no one *does* anything about it. The above discussion commits this same crime, but offers a reasonable working hypothesis which, it is hoped, will receive a proper test at the hands of experimental biologists.

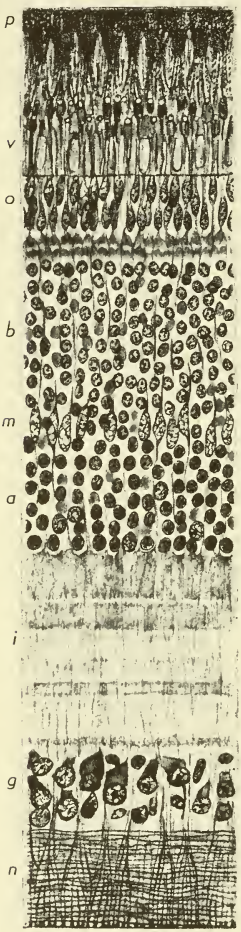
The Retina—The precision and elaboration of retinal layering reaches its peak in the birds. Scarcely a cell is out of place—*i.e.,* in a layer inappropriate to its type; and the inner nuclear and inner plexiform layers are more clearly differentiated into sub-layers than in other vertebrates with the possible exception of the prairie-dog. The fovea of the birds is the most perfect of all foveæ, and many birds have more than one in each retina.

The cells of the pigment epithelium are of the usual sauropsidan type, with numbers of fine processes, each containing a chain of bacilloid fuscin granules and extending as far as the inner segments of the visual cells. The latter are so slender and so tightly packed, and the ratio of conductive to sensory cells is so high, that all three of the nuclear layers and the inner plexiform as well (but not the outer) are relatively thick. The whole retina (whether diurnal or nocturnal) is thereby thickened—one and one-half to two times as thick as in vertebrates in general, and equalled only in some of the teleost fishes (compare Fig. 193a with Fig. 19, p. 43; note also Fig. 72, p. 177). Some sample nuclear-layer counts, made in the general fundus (away from the influence of any fovea present), follow:

Species:	Rows of: Outer nuclei	Inner nuclei	Ganglion cells
Week-old chick (*Gallus domesticus*)	2.5	18	2.5
Domestic pigeon (*Columba livia*)	3	15	2
Robin (*Turdus migratorius*)	3	28	3
English 'sparrow' (*Passer domesticus*)	3	12	2
Flicker (*Colaptes auratus*)	2.5	18	2
Marsh hawk (*Circus hudsonius*)	4	20	3
Red-tailed hawk (*Buteo borealis*)	3	17	2

The inner nuclear layer contains the bodies of many amacrine cells of several types, as well as a greater number of bipolars. The nuclei of the Müller fibers are much elongated in the direction of the retina's thickness, and form a single compact layer, within the inner nuclear layer, about one-half to three-fifths of the way through its thickness from the outer to the inner side. Outwardly from this line of Müller nuclei (toward the outer nuclear layer) are the bodies of the bipolars. Inwardly (toward the ganglion layer) lie those of the amacrines.

In the inner plexiform layer a variable number of faint bands can always be seen, running parallel to the retinal surfaces. These mark the distinct levels at which the various types of amacrines expand their terminal arborizations. At these same levels, for the obvious purpose of binding together the synapses at each level, there are varicosities on the filaments of the Müller fibers. These cells are very different from those of other retinæ, for in their course through the inner half of the retina they depart from the usual sponge-like structure, and each cell breaks up into a great



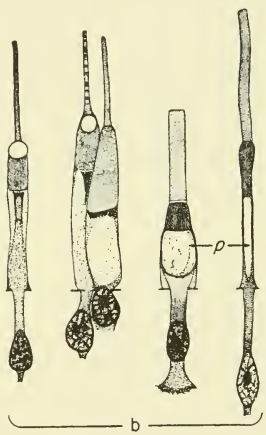


Fig. 193—The avian retina and its visual cells.

a, portion of fundal retina of week-old chick. ×500. *p*- pigment epithelium; *v*- visual cells; *o*- outer nuclear layer; *b*- bipolar elements of inner nuclear layer; *m*- row of Müller-fiber nuclei; *a*- amacrine elements of inner nuclear layer; *i*- inner plexiform layer (note stratification); *g*- ganglion-cell layer; *n*- nerve-fiber layer.

b, peripheral single cone and double cone, peripheral and fundal rods, of *Passer domesticus*. ×1000. *p*- paraboloid.

number of parallel threads, which terminate in an infinity of tiny trumpets to compose the tile-work of the internal limiting membrane.

The diurnal majority of birds have great numbers of single and double cones (their oil-droplets of divers colors, as in turtles), and relatively few rods. The rods may be restricted to the periphery or may even be entirely lacking in some instances. In nocturnal birds the rods predominate, though there may be large numbers of cones as well, some of them with pallid, though definitely pigmented, oil-droplets. The rod and cone nuclei and foot-pieces are of the same, 'cone', type in diurnal birds, but are differentiated in many or all nocturnal birds, as they are in other duplex vertebrates whose rods are numerous and very slender (teleosts, mammals). The rods of all birds contain rhodopsin.

These visual-cell types are pictured in Figure 193b (in their plump, easily-studied peripheral versions—compare Fig. 22e, p. 54). The avian cones are the same elements, phylogenetically, as their opposite numbers in the reptiles and the lower mammals (see Plate I). The bird rod has a paraboloid like those of chelonian and crocodilian rods, though it may be difficult to make out in the slenderized rods of the fundus, where it appears to form a long, slender tube. The rod is clearly comparable with the rod of the turtle, that of the alligator, and the cone of *Sphenodon* (see Figs. 176b, 177a, 179; pp. 612, 615, 621); but it has become a rod independently in the birds (or perhaps in their immediate ancestors—see Plate I), and is fully differentiated in the morphological sense only in nocturnal birds (*v.s.*).

The proverbial resolving power of the bird eye is based partly upon its large size and the relatively large image cast upon the retina, partly upon the dense concentration of the cones and the high ratio of optic-nerve fibers to visual cells. In the little white wagtail (*Motacilla alba*), outside the foveal region, Franz found approximately 120,000 visual cells and 100,000 ganglion cells per square millimeter of retina (compare the human *fovea*: 200,000—200,000). In an owl (*Bubo bubo*), with its relatively great summation, the corresponding figures were 56,000 and 3,600 (compare the overall summation-ratio of the human retina: *ca.* 125:1). *In* the fovea, even such birds as little *Passer domesticus* have 400,000 or more cones per square millimeter—and each cone presumably has its own bipolar and ganglion cells. The grand champion of all foveæ is perhaps that of a hawk (*Buteo buteo*), in which Rochon-Duvigneaud found 1,000,000 cones per square millimeter. Even outside the

fovea this hawk, with its approximately man-sized eye, has nearly twice the resolving power of human foveal vision; and, *foveally,* the visual acuity of some hawks and eagles reaches a value at least eight times that of man.

Chapter 18
MAMMALS

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The Class Mammalia contains three major divisions which are not serially related, but represent three branches from a single stem. The lowest mammals, closest to the reptiles, are the monotremes. These egg-laying forms include only the duck-bill or platypus (*Ornithorhynchus*) and the echidnas or 'spiny ant-eaters' (*Tachyglossus* and *Zaglossus* [=*Echidna* and *Proechidna*]). Ranking higher in point of specialization and anatomical distinctness from the reptiles, but not derived directly from monotremes like those now living, are the marsupials. These likewise have yolky eggs, but hatch them inside the body and bear the young alive in an embryonic condition. The young complete their development on a milk diet, outside the mother but usually inside an abdominal pouch. In the common opossum, *Didelphis virginiana*, the 'embryology' of the eye continues for 30-40 days after birth. The highest (placental) mammals nourish their young inside the mother's body by means of a 'placenta'. They were not derived *from* marsupials, but *with* them, as one of two branches.

(A) Monotremes and Marsupials

In these 'lower' mammals the eye alone would prove the reptilian origin of the whole mammalian class. Indeed, with the exception of exactly two features—one of them outside the eyeball (in the oculorotatory musculature) and the other one inside (in the ciliary body)—the monotreme eye is so completely reptilian that it affords no ammunition for use against those few mammalogists who claim separate reptilian origins for the monotremes and for all other mammals.

The marsupials originated as opossum-like animals, and only such forms (together with *Cænolestes*) have been able to survive in the American home of the group. In Australia however, where they became isolated from placental flesh-eaters, the marsupials differentiated into a number of types, many of them imitative of placental types. Thus, there are *marsupial* mice, rats, marmots, rabbits, flying-squirrels,* jerboas, bears, cats, wolves, ant-eaters, and golden moles. There was once even a marsupial 'lion', though it was probably a mild-mannered vegetarian. The marsupials have avoided the water, so there are no marsupial seals or porpoises—the tropical American water-opossum, *Chironectes,* is the only aquatic marsupial. Nor have the marsupials developed any hoofed types; but the larger kangaroos fill about the same ecological niche.

The lower marsupials are mostly carnivorous and the higher types (phalangers, kangaroos) herbivorous. Most marsupials, like the monotremes, are crepuscular or nocturnal to some degree; but the larger kangaroos are arhythmic and a few are quite strongly diurnal. In keeping with the adaptive radiation of the marsupials, their eyes show great differences from form to form. In proportion to the number of species, they have had woefully little attention as compared with the placentals. The marsupials are really the central group of mammals, and deserve much more thorough exploration, from *all* biological viewpoints, than they have ever yet received.

The Monotreme Eye—The eye of *Ornithorhynchus* has been described only once, by Gunn in 1884 from material preserved in whisky by a Mr. Sinclair, who clearly took his science very seriously. The eyes of the two genera of echidnas have been described by Franz, by Kolmer,

*A fascinating coincidence is that the flying-squirrel type has been evolved more than once in the rodents—by the true flying-squirrels and in the Anomaluridæ—and more than once also in the marsupials: there are three kinds of flying phalangers, each a close relative of a different non-flying form.

and by Gresser and Noback. None of these accounts is entirely accurate —all incorporate particularly serious errors in regard to the shape of the globe (which is 'avian' only when collapsed) and the presence of a ciliary muscle (which is wholly lacking, though two of these authors describe it as having the same three types of fibers—meridional, 'radial', and circular—as the ciliary muscle of man). The ensuing descriptions are based upon preparations of *Tachyglossus* and *Ornithorhynchus* made by Kevin O'Day, and upon correspondence with him. Statements of earlier workers which happen not to be refuted by O'Day's splendid material are also incorporated.*

Ornithorhynchus has an excellent nictitating membrane. *Tachyglossus* has none; but both genera have retractor bulbi muscles. The lids are plump and small in both, and in *Tachyglossus* are closed by swinging rather than by sliding. Small Meibomian glands, still with relation to hair follicles, are present in *Ornithorhynchus*. These may be orimentary (see p. 40); but the same situation occurs in one placental, the hedgehog (*Erinaceus*). They are lacking in *Tachyglossus* and *Zaglossus*. Like most Sauropsida, *Tachyglossus* has a tarsus in the lower lid only, while *Ornithorhynchus* has one in each lid. Both genera are supposed to have both lacrimal and Harderian glands (but Kolmer found only serous glandular tissue in *Zaglossus*). The adnexa in *Ornithorhynchus* thus show no specialization for the amphibious life of the animal. In fact, those of the echidnas exhibit rather more reduction, which seems largely explained by the presence in those forms of a keratinization of the corneal epithelium, no doubt in adaptation to the ant-eating habit (as in armadillos and aard-varks).

In the arrangement of the superior oblique muscle, the monotremes are wholly 'mammalian'. In the echidnas there is a slip which runs from the old sub-mammalian origin (on the anterior nasal orbital wall) to an insertion on the globe; but merging in this same insertion is a second slip, muscular almost to the globe, which comes through a pulley from an origin only a few millimeters anterior to the deep point-of-origin of the four recti. The duck-bill has only this long portion, and moreover has it as in higher mammals, *i. e.* originating with the recti and becoming

*Dr. O'Day has been trying for several years to find time to prepare a monograph on the eyes of the monotremes. When this does finally appear it will greatly extend, and no doubt partially contradict, the present treatment. In the meantime, because of the slowness and uncertainty of communication with Australia, the writer has made bold to discuss O'Day's findings without seeking his permission—they seem much too important to be left out of this book.

tendinous before reaching the pulley, with the latter chondroid rather than soft as in the echidnas. This seems too strong a similarity to the higher mammals to be dismissed as a coincidence by those who consider the monotremes to have originated from a separate reptilian stock. It is not certain what called forth the elongation of the mammalian superior oblique. Such an elongation *may* have occurred twice. In this connection, it would be nice to know whether the optic chiasmata of the monotremes are only partially decussated. Both types have wide binocular fields, that of the echidnas being projected forward and that of the duck-bill largely upward.

The eyeball is usually figured with a short axis and a pronounced circumcorneal scleral sulcus, both of which are collapse-artefacts. Correspondingly, its shape has most often been called 'avian'.* Actually, the eyeball is everywhere convex and is spherical in all monotremes. This sphericity, so reminiscent of the snakes, has the same basis—a total disappearance of the ancestral scleral ossicles (Fig. 194a).

The eyeball of *Tachyglossus* is eight or nine millimeters in diameter, that of *Ornithorhynchus* about six. In all monotremes the sclera contains the cartilage cup with which we have become so familiar in preceding chapters. In *Tachyglossus* the cartilage is 27μ thick in the region of the optic nerve, 14μ thick near its sharp anterior lip. In *Zaglossus* (a larger animal) it averages 160μ in thickness. In the duck-bill it is even thicker fundally (400μ) but tapers to 25μ near its knife-edge termination. The cartilage reaches to the posterior ends of the ciliary processes in *Ornithorhynchus,* but stops opposite the ora terminalis in *Zaglossus* and a little behind the ora in *Tachyglossus*. An outer layer of fibrous scleral tissue about equal in thickness to the cartilage (but only 96μ in *Zaglossus*), continues forward (receiving an addition which replaces the cartilage) through a zone formerly occupied by the scleral ossicles, and blends with the substantia propria of the cornea. In *Tachyglossus* at least, an outer fraction of the substantia propria is easily seen to be continuous with the conjunctival corium or 'episcleral' connective tissue. A loose layer of episcleral blood vessels, from which capillaries

*And all the sauropsidoid internal features are likewise called avian by those who are familiar with their occurrence in birds but ignorant of their occurrence also in the reptiles. Attempts to derive the monotreme eye from the avian, and coy insinuations that the two eyes are identical through convergence (justifying the 'bill', webbed feet, spurs, and egg-laying habit of the platypus), are naïve in the extreme; but they continue to be made.

The astute Franz indicates in several places that he suspects that the 'avian' form of the usual preserved echidna eye is a result of collapse. O'Day finds that this collapse occurs very readily in both *Tachyglossus* and *Ornithorhynchus*.

are sent into the cornea for some distance, marks the boundary. Nowhere else above the teleosts is it so readily to be seen that an outer portion of the substantia propria is homologous with the dermis rather than with the dura (Fig. 194a; *cf.* Fig. 151, p. 451). A Bowman's membrane has been claimed for *Ornithorhynchus,* but none can be made out in *Tachyglossus.* Both these genera have the usual Descemet's layers, but Kolmer could not make out the elastic membrane in *Zaglossus.*

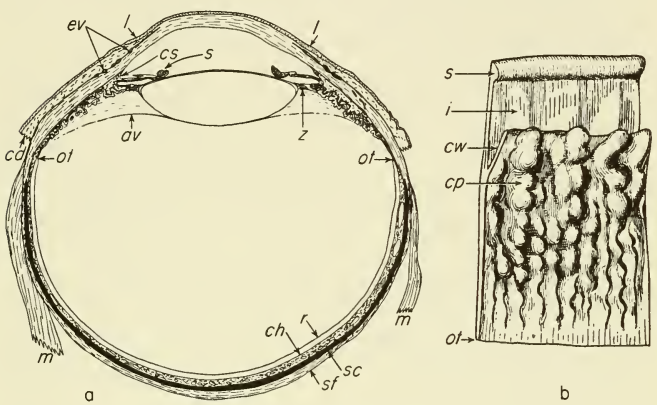

Fig. 194—The monotreme eye.

a, section of eye of *Tachyglossus* sp. ×8. Drawn from a preparation of O'Day.

b, inner surface of segment of anterior uvea of *Tachyglossus.* After Franz.

av- anterior surface of vitreous; *cd-* conjunctival dermis; *ch-* chorioid; *cp-* ciliary process; *cs-* canal of Schlemm; *cw-* ciliary web; *ev-* episcleral vessels, marking boundary between dermis and fibrous tunic; *i-* iris; *l, l-* external limits of cornea; *m, m-* rectus muscles; *ot, ot-* ora terminalis retinæ; *r-* retina; *s-* sphincter; *sc-* scleral cartilage (black); *sf-* fibrous layer of sclera; *z-* zonule (main portion).

In keeping with its aquatic habits the duck-bill has a relatively broader cornea than *Tachyglossus,* but it has a deeper anterior chamber (cornea 4.0mm. in diameter in a 6.0mm. eye, *vs.* 3.4mm. in a 8.0mm. eye; chamber 1.25mm. deep *vs.* 0.9mm.). The duck-bill's corneal substantia propria is only one-fourth as thick as the echidna's, but its epithelium is much thicker and nearly equals the propria—such thickening being highly characteristic of aquatic vertebrates in general. The duck-bill cornea is 100μ thick peripherally, only 55μ apically. *Zaglossus* reverses this rela-

tionship, with its whole cornea 320μ thick centrally (with 264μ of propria) and 540μ peripherally (460μ of propria). Comparable figures for *Tachyglossus* are 350-290, 330-210.

The chorioid is only 50μ thick in the duck-bill, a little more than twice this thick in *Tachyglossus*. Histologically, it is ambiguous—as turtle-like as it is 'mammalian'. The pigmented, laminated suprachorioidal layer or 'lamina fusca' is conspicuous, as is the choriocapillaris, whose elements are unusually large in lumen and are readily seen to be connected with the large veins.

In all three genera the iris is most simple, its web consisting of little more than the two heavily pigmented retinal layers and a few small blood vessels attached loosely to the anterior face. There is no dilatator, but there is a massive sphincter around which the pigmented retinal layers are rolled so that their mutual edge lies on the anterior face of the iris. The root of the iris lies opposite the limbus in the duck-bill, but well back of this landmark in the echidnas. There is no pectinate ligament; but, as in reptiles which lack one, there is a thin anterior continuation, past the iris root, of ciliary-body connective tissue, which is adherent to the inner surface of the fibrous tunic and tapers to a knife-edge aligned with the peripheral margins of the Descemet's layers. The canal of Schlemm is embedded in this uveal meshwork tissue, as it is in sauropsidans in general. The iris is dark brown in life, the pupil always circular.

The anterior continuation of the chorioid forming the uveal portion of the ciliary body is thin, only lightly pigmented, and not sharply demarcated from the inner layers of scleral fibers except where it underlies the tallest portions of the ciliary processes. There is no trace of a ciliary muscle, and the writer is quite unable to imagine what it may be that others have mistaken for one. The ciliary processes are low, puffy, and tortuous, and number about 60 in *Tachyglossus*. Their anterior ends are interconnected by an annular shelf-like structure—like a miniature iris—the 'sims'. This German term has never been translated; perhaps it is high time that it was. Since the sims connects the ciliary processes, which give the ciliary body its name (cilia = hairs or threads), after the fashion of the webbing which connects the toes of a duck or a frog, it will be called here the 'ciliary web' (Fig. 194b, *cw*).

The ciliary web is a decidedly mammalian character, shared by many marsupials and placentals but by no sauropsidans. Every *other* feature of the monotreme eyeball—whether the feature is a structure, or the

absence of a structure—occurs in some living reptilian group. The ciliary web alone* thus keeps the eye of the monotreme from being entirely reptilian, with its closest morphological resemblance to the eye of the likewise-nocturnal crocodilian.

The lens is unexpectedly small, flat, and anterior in position. The topography of the monotreme anterior segment, particularly in the echidnas, is in fact not at all sauropsidan but more like that of the sirenians and primates. *Tachyglossus* has the flattest of all lenses, with a flatness-index (diameter divided by thickness) of 2.75.† This value is closely approximated elsewhere only in some of the higher primates, including man (*ca.* 2.7). At its equator, the lens epithelium is twice as tall as at the anterior pole, constituting perhaps a vestigial ringwulst. A similar situation obtains in the duck-bill, and also in some marsupials. The lens of the duck-bill, in keeping with the aquatic habit, is much less flat—2.66/1.93 = 1.38 (Kahmann), 2.45/1.75 = 1.4 (Gunn), or 1.5 (from a photograph of O'Day's—scale not given). O'Day compares its form with that of the lens of the local Murray turtle, *Chelodina longicollis*.

No monotreme has any demonstrable accommodation, and there are no reports as to refractive conditions. It is not known whether *Ornithorhynchus* approaches emmetropia in either air or water, but the implications are that the eye is better adjusted to the latter medium. The echidna eye looks as though it must be extremely hypermetropic; but only a study of the living animal can settle the matter.

In both *Ornithorhynchus* and *Tachyglossus* the numerous zonule fibers arise from the coronal zone of the ciliary body and from the free portions of the ciliary web (including its very edge), and insert compactly on the extreme periphery of the lens, largely just in front of its equator.

The Monotreme Retina—The rather thin sensory retina extends farther forward temporally than nasally in *Ornithorhynchus* (but not in *Tachyglossus*?), suggesting an importance of the binocular field.

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*And the unstriated condition of the sphincter pupillæ; but there is no reason to think that this is a *new* muscle. Iris muscles have been independently evolved several times of course; but the mammalian sphincter has, in all probability, been inherited directly from the reptiles. Not so the mammalian dilatator.

†Measured in O'Day's preparations (3.3mm / 1.2mm.); Franz gives 3.0 / 0.8 = 3.7, but expresses doubt as to the validity of these figures. Kolmer gives 2.88 / .96 = 3.0 for *Zaglossus*, but his material was preserved many hours post mortem.

There are no blood vessels either in the retinal tissue (as in a few marsupials and many placentals) or lying on its surface like the hyaloid or vitreal systems of lower vertebrates. No monotreme has any trace of a conus papillaris. This complete nutritional dependence of the retina upon the chorioid is characteristic of light-shunning vertebrates (see pp. 648-58). The disc is small, smooth, and unpigmented in both genera, circular in *Ornithorhynchus* and vertically oval in *Tachyglossus*. Kolmer describes a peculiar mass of connective tissue which is embedded in the bulbar portion of the optic nerve in *Zaglossus*.

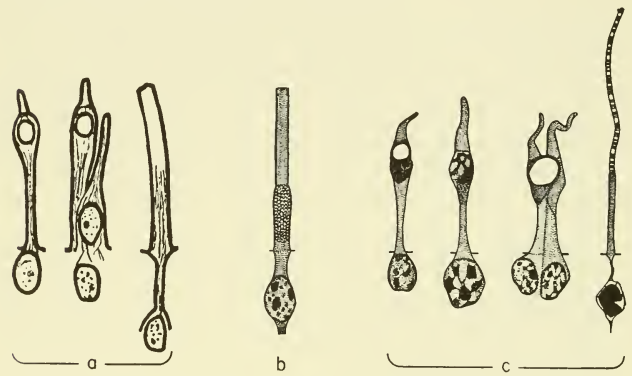

Fig. 195—The visual cells of the lower mammals. ×1000.

a, single cone, double cone, and rod of *Ornithorhynchus*. After O'Day.

b, element from pure-rod retina of *Tachyglossus*. Drawn from a preparation of O'Day.

c, droplet-bearing and droplet-free single cones, double cone, and rod of an opossum, *Marmosa mexicana* (Australian marsupials have no droplet-free cones and have droplets in both members of their double cones).

Not only in its avascularity, but in its entire histology, the monotreme retina is sauropsidan and might easily be taken for that of a nocturnal reptile. In *Ornithorhynchus,* O'Day figures three rows of outer nuclei, four of inner, and a single row of ganglion cells, and says that the nerve-fiber layer is thin even near the disc. *Tachyglossus,* which is pure-rod, has three layers of outer nuclei (*Zaglossus* has four), only two of inner (*Zaglossus* has three), and a decidedly scattered single row of ganglion cells. Some of the latter are ectopic and lie at various levels in the inner plexiform layer. The greater extent of summation in the

echidnas, and the total absence of cones,* implies a stricter nocturnality than that of the duck-bill; but no great difference in habits seems to have been noted.

The types of visual cells are direct derivatives of those of the Sauropsida (Fig. 195a, b; *cf.* Figs. 176b, 177a, 193b, pp. 612, 615, 660; and see Plate I). In *Ornithorhynchus* the single and double cones have lost the paraboloid but have retained the oil-droplet, which was very recently found to be colorless. The rod and cone nuclei are not differentiated, but are both 'cone-like' as in all sauropsidans excepting nocturnal birds. In *Tachyglossus* the cones themselves have gone. The complete monotreme visual-cell pattern (of *Ornithorhynchus*) fits equally well the accepted idea that the monotremes are a lateral branch of the stock which culminated in the marsupials, and the minority notion that the monotremes evolved independently from reptiles. The simplification of the cones in the duck-bill, and their discard in the echidnas, are natural consequences of adaptation for dim-light activity.

The Marsupial Eye—Marsupials have a nictitating membrane, but it is never highly developed. Its gland (the Harderian) is present, along with the lacrimal. A retractor bulbi is present; but no details are on record concerning the extra-ocular muscles.

The eyeball is perfectly spherical in a very few species and is practically spherical in all others. The horizontal and vertical diameters are always equal, and usually exceed the axial length (by up to 10%). This relationship is reversed in some opossums. The topography of a sagittal section is always like that in nocturnal and arhythmic placentals (Fig. 196a; *cf.* Fig. 71, p. 173). The diameter of the cornea is always great in proportion to the diameter of the eyeball—66-80% in kangaroos, 82% and 87% in opossums (*Didelphis virginiana* and *Marmosa mexicana* respectively), 91% in the cuscus (*Trichosurus vulpecula*). The cornea is horizontally ovoid only in large kangaroos, in simulation of their ungulate counterparts.

The sclera is fibrous, entirely devoid of cartilage (except for some questionable nodules in the marsupial 'golden mole', *Notoryctes*). It has thus taken the final step in the elimination of the cartilage-and-bone system of the reptilian eyeball wall, and the basically spherical form of the marsupial eyeball is the expression of this elimination (*cf.* snakes).

*Certain in the case of *Tachyglossus;* probable in *Zaglossus,* but Kolmer's material was too badly histolized to make possible any study of the visual cells.

Wherever in higher (*i e.,* placental) mammals the eye departs from this fundamental sphericity and gains the *appearance* of having a circumcorneal scleral sulcus, it is owing to the production of a cornea whose radius of curvature is substantially less than that of the sclera (*e. g.,* man).

The cornea has a 4-5-layered epithelium, and no Bowman's membrane; but Descemet's membrane is ordinarily very thick (not, however, in *Marmosa*). The cornea is usually uniform in thickness throughout, but is thinned peripherally in opossums and perhaps in other small-eyed forms.

The chorioid is usually about as thick as the sclera—hence, thin in small eyes and thick in large ones. It is heavily pigmented, richly vascular, and ordinarily is built quite as in the placentals. In *Didelphis,* however, a choriocapillaris is present only in the pouch young. During growth to adulthood, *pari passu* with the maturation of the tapetum formed from the retinal pigment epithelium and the unusual invasion of the outer nuclear layer by retinal capillaries, the choriocapillaris is replaced by (or becomes) a plexus of plump, thin-walled veins which occupy the same position against the back of the glass membrane. These alterations bespeak a turning of the visual cells from the chorioid to the retinal circulation as their source of supplies, owing to the impermeability of the tapetum. In a very few other marsupials (*Dasyurus, Thylacinus,* possibly *Sarcophilus* and *Petaurus*) the chorioid is modified by the presence of a tapetum fibrosum. In *Dasyurus viverrinus* this nearly fills the chorioid—squeezing the large vessels and the few thin, pigmented lamellae out against the sclera—and runs practically from ora to ora, though permitted to reflect light back through the retina only in the superior half of the eyeground, where the retinal pigment epithelium is devoid of pigment. It is probably significant that it is only in *Dasyurus, Sarcophilus, Didelphis,* and *Marmosa* (which may once have had a tapetum like its close relative *Didelphis*) that any retinal vessels are known to occur—necessitated, apparently, by the interference of the tapetum with the nourishment of the retina by the chorioid (see pp. 652-4). A vestigial conus papillaris may also occur in marsupials (*Perameles, Hypsiprymnus,* and kangaroos generally). The supply of the retinal capillary bed, where present, is from paired veins and arteries which radiate over the retina from the disc. In *Dasyurus viverrinus* each of these veins (and their larger branches) is triangular in cross-section and is embedded in the inner layers of the retina, with its round arterial companion lying on

top of it in a low glial ridge which projects a trifle into the vitreous.

The iris contains an unstriated sphincter near the pupil margin (as in other mammals); but no marsupial is known to have a dilatator. Both retinal layers are therefore heavily pigmented. The stroma is likewise densely pigmented and is richly vascularized, often with many vessels partially extruded from its anterior surface.

In large eyes the ciliary body forms a broad zone with well-marked orbicular and coronal regions; but in small eyes, whose lenses are enormous, the ciliary body is reduced about as it is in snakes. In large eyes

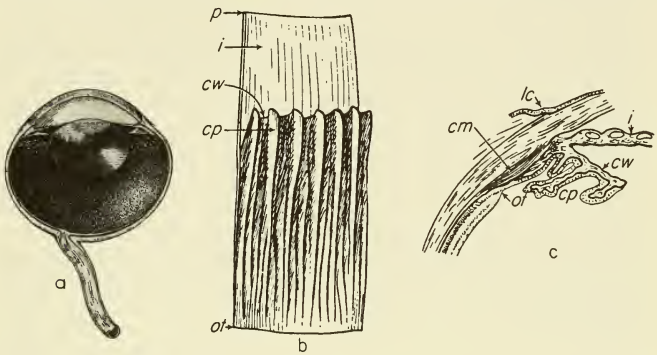

Fig. 196—The marsupial eye.

a, ventral half of left eyeball of a kangaroo, *Macropus giganteus*. ×1. After Soemmerring.

b, inner surface of segment of anterior uvea of a kangaroo, *Macropus agilis*. After Franz.

c, iris-angle region of cuscus, *Trichosurus vulpecula*. Redrawn from Franz.

cm- ciliary muscle; *cp*- ciliary process; *cw*- ciliary web; *i*- iris; *lc*- limbus corneæ; *ot*- ora terminalis retinæ; *p*- pupil margin.

the ciliary processes are regular, tall, and thin (Fig. 196b); and they are about as numerous as in comparable placentals (*e.g.*, 120 in *Trichosurus*). Those of small eyes are low, tortuous, and not so readily counted. A ciliary web can usually be made out. Though no marsupial has yet been demonstrated to have any accommodation whatever, a small ciliary muscle is always present. This may present itself as a meridional Brücke's muscle with exactly the same relationship to the corneal margin as in reptiles (Fig. 196c, *cm*). More often, apparently, it contains both circular and meridional fibers. The circular ones occupy the anterior half

of the muscle in *Dasyurus* and *Marmosa,* and in the former genus they lie toward the scleral side of the muscle. In *Didelphis* the meridional and circular fibers are intermingled in small bundles. The anterior tendon in these three genera, and probably in many others, is formed by a small mass of unpigmented uveal 'meshwork' tissue which lies against the anteriormost part of the sclera and extends forward beyond the iris root, where it tapers to meet the edge of the membrane of Descemet. Between this tissue and the sclera lies the endothelial canal of Schlemm. These relationships are essentially those of the human eye. Within the marsupial group, then, the ciliary muscle may be situated either as it is in reptiles, or as it is in placental mammals. The transition seems to be made simply by the creation of the meshwork 'tendon', dropping the anterior end of the muscle farther back from the limbus corneæ.

The lens is always relatively large; and in the smaller, more strongly nocturnal types it may nearly fill the globe—as in many small-eyed nocturnal placentals, *e.g. Mus.* The flatter lenses occur, as would be expected, in the large-eyed arhythmic forms (Fig. 196a; compare Fig. 71 [opossum], p. 173). Even in the flattest lenses there are never more than traces of the reptilian ringwulst, and the lens is always quite out of contact with the ciliary processes. The flatness index of the lens may be little more than 1.0, or as high (in kangaroos) as 1.5. Some sample values follow:

Species	Horiz. ϕ of eye	Lens ϕ (D)	Lens Thickness (T)	Index (D/T)
Marmosa mexicana (a mouse opossum)	6.3mm.	4.7mm.	4.5mm.	1.05
Didelphis virginiana (the common opossum)	11.0	7.3	6.0	1.22
Dendrolagus bennetti (a tree kangaroo)	15.0	8.3	6.7	1.24
Osphranter (*robustus*?); (a rock dwelling kangaroo)		13.0	10.0	1.30
Macropus giganteus (a ground kangaroo)	27.0	13.0	10.0	1.30

The Marsupial Retina—Through its loss of all of the accessory structures involved in sauropsidan accommodation (except the ciliary processes—and these no longer bear upon the lens), the marsupial eye as a whole is thoroughly mammalian—*i.e.,* placentalian. The retina,

however, is as reptilian as that of the monotreme. The visual-cell types are the same ones as in *Ornithorhynchus*—single and double droplet-bearing cones, and filamentous rods (which always outnumber the cones very greatly, in contrast to *Ornithorhynchus*). Only minor modifications of the full monotreme pattern occur in marsupials. Thus in the American opossums some of the single cones lack oil-droplets (see Fig. 195c, p. 670); and in all Australian marsupials so far examined by O'Day, the double cones have oil-droplets in *both* their members—a curious situation which occurs in American marsupials (and in some birds) only as an occasional anomaly.*

The rod nuclei in marsupials contain only one or two chunks of chromatin—a differentiation, from the larger and open nuclei of the cones, which is characteristic of the placentals but not of the monotremes. It is not known whether the rod and cone foot-pieces are also differentiated in marsupials. The cones of marsupials, like those of all other mammals, lack paraboloids. This seems a point of some value in defense of the monophyletic derivation of all the mammals from a single reptilian stock.

The single and double cones of marsupials and monotremes, from their oil-droplets (and despite their loss of the paraboloids), are clearly the 'same' elements as the corresponding ones of the reptiles. The monotreme-marsupial rod is left to be homologized with the droplet-free element of the sauropsidans (see Plate I). Its increased (nuclear) differentiation in the marsupials, over that in the monotremes, coupled with the persistence of the useless oil-droplets in both groups (these are gone entirely in the placentals!), suggests that the ancestral monotremes and the original marsupials were diurnal, and that the monotreme-marsupial line acquired its rods secondarily through transmutation and perfected them within the confines of the line (*cf.* reptiles, birds).

(B) Placentals

The earliest placentals were 'insectivores' of the *Deltatheridium* type. In the Mesozoic, these primitive forms diversified and established several separate lines of ascent. The insectivore type itself persisted (giving off the still extant Lipotyphla and, later, forms ancestral to the whales) and culminated in the 'creodonts'—archaic carnivorous forms, of which the

*According to Albarenque, *Didelphis marsupialis* and '*Azara*' (= *D. azarae*?) have only rods. This seems improbable in view of the extremely close relationship of these forms to *D. virginiana*.

modern orders Carnivora and Pinnipedia (seals) are fairly direct descendants. From pre-creodonts, there diverged a line which produced the artiodactyl 'ungulates'* (peccaries, pigs, hippopotami, tylopods [camels etc.], deer, antelopes, cattle).

The Lipotyphla (hedgehogs, tenrecs, otter-shrews, shrews, moles, golden moles etc.) comprise the larger of the two groups of *living* insectivores. From this stock diverged the smaller branch called the Menotyphla, the living members of which comprise the tree-shrews and elephant-shrews. Along the way, the Menotyphla gave off a branch which bifurcated into the Dermoptera (taguans or 'flying lemurs'—*Galeopithecus* and *Galeopterus*) and the Chiroptera (bats). The order Primates also branched off from menotyphlous stock, close to the tree-shrews; and the latter, like the higher primates, have secondarily become diurnal—perhaps the most primitive placentals to have done so.

From a second of the groups of Mesozoic insectivore-like forms, the rodents and lagomorphs arose. In their highest specializations, the rodents have risen above some other groups whose origins were not as ancient.

A third assemblage of Mesozoic forms gave rise to the modern Xenarthra, comprising the sloths, armadillos, and ant-bears. To these American forms the African pangolins or 'scaly ant-eaters', the Nomarthra may be closely related. The Xenarthra and Nomarthra, *if* they are thus related, form a natural order, the Edentata; otherwise the Nomarthra, deserve ordinal rank. To the 'edentates' in a former, looser sense, the Tubulidentata (now considered quite unrelated) were once assigned.

The Tubulidentata, represented today only by the aard-varks (*Orycteropus* spp.), the hyracoid-proboscidean-sirenian bouquet, and the perissodactyl ungulates (horses, zebras, tapirs, rhinoceroses) are all derivatives of pro-ungulates which flourished in Cretaceous time and radiated from still a fourth branch of the Mesozoic radiation of insectivore-derivatives.

The Eye as a Whole—In so diversified a group of vertebrates—in contrast to the birds—the eye naturally exhibits a profuse adaptive

*The mammalogical reader will have noticed that throughout this book the old term 'ungulate' has been employed. It embraces several orders which are of course widely separated in modern classification: the Artiodactyla (even-toed) and the Perissodactyla (odd-toed hoofed forms), the Hyracoidea (hyraxes) and their close relatives the Proboscidea (elephants). (The Sirenia, though never classed as 'ungulates', are connected with the base of the elephant branch). The nowadays artificial term 'ungulate' has seemed here a convenient word-saver, for the orders embraced by it have eyes which are much alike. From comparative ophthalmological evidence, no one would be led to believe that the artiodactyl and perissodactyl lines of descent have actually been separate since almost the inception of the Placentalia.

radiation paralleling that of the group itself. The placental-mammalian eye has been carried along the ground—rapidly or slowly—and into trees, into the free air, into the fresh waters, and a mile below the surface of the ocean. It has been required to work in brightest sunlight and faintest starlight. It has been asked to inform its owner of an enemy miles away, and to analyze a tiny object held close before the face. The placental eye has been able to cope with all of these situations. Only in complete and permanent lightlessness has it given up, and shrivelled to a pin-head hidden beneath the skin. This sort of degeneration has occurred several times—in two distinct families of lipotyphlous insectivores, the true, talpid moles (*Talpa, Scalopus,* etc.) and the golden moles (*Chrysochloris* spp.); in two families of rodent 'moles', the Spalacidæ and the Bathyergidæ; and in one additional genus of rodent (*Ellobius*) which belongs to the hamster branch of the mouse family.

The adnexa have been discussed on pp. 36-41 (man) and pp. 425-8 (mammals in general); and the special features of the sirenians, whales, and seals have been previously treated (pp. 407-17, 444-8). There remains a great deal which could be said about placentalian eyes, not much of which can be squeezed into the space allotted here. For detailed anatomical information the reader will have to turn to such compendia as that of Franz (1934), and to the works cited therein.

Functional, harmonious, placentalian eyes range in size from about a millimeter in the shrews and the smallest bats to that of the great blue whale, *Balænoptera musculus* (145 × 129 × 107mm.). Carnivores, diurnal primates, and ungulates have the largest eyes relative to body size. In the lowest orders (Insectivora, Chiroptera, Edentata, Rodentia) the eye is both relatively and absolutely small, in sympathy with the nocturnality of these animals and the unimportance of vision in their lives. *Orycteropus* however has a large eye (22 × 22mm., 20.5mm. axis), which aligns this form with its ungulate relatives.

The basic shape of the eyeball is the sphere; but a horizontal ellipsoidality, at maximum about as great as it ever is in birds, occurs in some ungulates and in many large-eyed aquatic forms. The cornea may protrude from the sphere formed by the rest of the globe when it is small and sharply curved throughout (*e.g.,* man), or its apex may be acutely curved even though the rest of the cornea blends with the curvature of the sclera (carnivores). The axis is somewhat shortened in many ungulates, in which the lens has been moved forward (see Fig. 71, p. 173), and also in the more fish-like aquatic eyeballs. In *Galago* and *Tarsius,*

and to a lesser extent in some other nocturnal prosimians (*e.g., Nycticebus*), the eye is 'tubular' (Fig. 84, p. 213). In large-eyed mammals, it is common for the lens and cornea to be shifted nasally as in birds, and for the ciliary body to be consequently narrower nasally than temporally, chiefly at the expense of the nasal orbiculus, which may be quite abolished (see cougar, Fig. 71).

The sclera never contains any traces of cartilage. It is usually thickest in the fundus and thinnest at the equator; but the cornea may be much thicker than any part of the sclera, or much thinner—the local differences in the thickness of the fibrous tunic are so various that they cannot be covered in a few words. A Bowman's membrane is seldom discriminable; but Descemet's layers are always present, and the elastic membrane may be enormously thick in large eyes. An exceptional cornea is that of the armadillo (*Dasypus novemcinctus*), in which the substantia propria contains many capillaries, even at the apex. These are perhaps required by the fact that the corneal epithelium, being strongly keratinized, can derive no sustenance from the tear fluid.

Except where a tapetum lucidum has been produced in it, the chorioid is usually built as it is in man, but is seldom so thick. It is exceptionally thin in the squirrel family; but the most unusual chorioid is that of the large bats (Megachiroptera). In these forms there are 20,000-30,000 conical, vascular papillæ which are protrusions of the chorioid, interdigitated with the retina and deforming the latter's visual-cell layer (see Fig. 102a, p. 255). Kolmer found this situation in all sixteen of the species he studied, but not in any of an equal number of microchiropteran species. Five structural types of papillæ can be recognized; and more than one type may occur in one species, in different retinal regions.

The iris in large eyes (carnivores and seals, ungulates, whales, primates) has essentially the same constituents as in man. All of these mammals have a dilatator, histologically and embryologically resembling that of man, but with a topographical arrangement which depends upon the shape of the contracted pupil (see Fig. 85, p. 218). In well-adapted aquatic placentals (otters, seals, whales), and also in the pigs, the sphincter occupies the entire width of the iris; and the dilatator may send fibers into the ciliary body for firmer anchorage. In the smaller, nocturnally-adapted eyes of all the lower orders of placentals, a dilatator is ordinarily lacking; but the sphincter is always in evidence and sometimes very large, though always compactly massed near the pupil margin. Toward the root of the iris, stromal strands may cross the filtration

angle and join to the cornea, thus contributing to the 'pectinate ligament' (or sometimes forming the whole of it). At the other 'end' of the iris—the pupil margin—cystic protrusions of the pigmented retinal layers form the corpora nigra or 'grape-seed bodies' (Fig. 86, p. 219) which are characteristic of the highest artiodactyls (tylopods, and ruminants except *Tragulus*) and also of the highest perissodactyls (horses). Where a dilatator is present, the anterior retinal layer is pigmented only slightly or not at all; otherwise, it is as dark as the posterior layer, as in lower vertebrates in which it has not partly differentiated into muscle. The color of the iris is usually dark brown. Where it is not, the color is generally optical, as in the 'blue' human eye; but lipophores and iridocytes may be present in the stroma, as in the cats and some prosimians.

The organization of the ciliary body in all placentals is basically the same as has been described earlier for man. A corona (bearing true, vascular, ciliary processes) and an orbiculus (smooth, or bearing only low meridional ridges) can usually be distinguished. In carnivores however, the posterior ends of the processes are practically at the ora (Fig. 197, p. 683); and in *Orycteropus* and ungulates, whose corneæ are markedly ovoid horizontally, the obligation of the coronal zone to remain circular (to 'fit' the lens) results in an encroachment upon the iris, nasally and temporally, by the anterior ends of the processes—so that these portions of the iris serve as extensions of the base-plate of the ciliary body, and are rendered immobile as regards changes involved in the operation of the pupil. In ungulates and in many carnivores the orbiculus is practically eliminated nasally owing to the existence of marked nasad asymmetry (see p. 300).

Except in very small eyes, the main part of the ciliary body (apart from the processes, that is) gradually thickens toward its anterior end, as in man. This bulk of uveal tissue is not, however, solid muscle as in the primate eye. Muscle—sometimes considerable of it, as in carnivores—is almost always present, but is in the form of slender fascicles interspersed with much connective tissue. Anteriorly, the ciliary muscle tends to have two anchorages: one, by means of the meshwork tissue which terminates at the margin of Descemet's membrane (as in man—see Fig. 5, p. 10), and another attachment into the anteriormost portion of the base plate, practically in the root of the iris. Between these two anterior leaves of the muscle lies a nearly empty space, best visualized by imagining the human filtration angle to be eroded or extended backward deep into the ciliary body. This space, 'Fontana's space(s)', is traversed by

delicate strands of uveal tissue which join the base-plate to the sclera. The anterior limit of Fontana's space—its boundary with the anterior chamber (with which it is of course actually continuous, between the strands)—is fixed by the strands or struts which make up the true pectinate ligament: These are heavy connective-tissue fibers, coated with mesothelium, which run from the limbal region of the fibrous tunic to the root of the iris, and support the latter against the tug of the part of the ciliary muscle attached thereto, and the pull of the sphincter during the partial closure of the pupil which ordinarily occurs during accommodation. The pectinate ligament gets its name from the word 'pecten', meaning 'a comb', and referring to the fact that its strands are like the teeth of a comb which has been bent into a circle with the teeth pointing inward. The strands are best developed in horses, artiodactyls, *Orycteropus,* carnivores, and especially in seals (where there may be not one 'tooth' but several in a given meridian, forming a fan, somewhat like the situation in reptiles (see Fig. 109, p. 275; Fig. 71, p. 173 [lynx, cougar, dog, dromedary]; and Fig. 150, p. 446). In the horse at least, they appear to be continuous with and identical with the material of Descemet's membrane; and the horse has very similar fibers, with a *circumferential* course, massed anteriorly in the meshwork of the iris angle.

In small, large-lensed eyes with very extensive corneæ (in murids and similar rodents, armadillos, etc.) the whole ciliary body is reduced greatly and occupies a relatively narrow zone—sometimes, as in shrews, forming a simple roll without meridional folds or ridges, quite as in the snakes. The uveal meshwork tissue, covering the canal of Schlemm and tapering to meet Descemet's membrane, which so often serves as a tendon of the ciliary muscle, is still present in these eyes; but the ciliary muscle is usually wholly lacking. Fontana's space is either tiny, or else is confluent with the anterior chamber owing to the absence of a pectinate ligament (as also in some large eyes, *e.g.* the human). Such eyes have no accommodation; and for that matter none has ever been convincingly demonstrated for ungulates—domestic ones, at any rate—despite the presence of considerable tissue of supposedly contractile character. In these small eyes, the ciliary processes are so blobby and irregular that they can scarcely be counted. A very different situation exists in large placental eyes:

The ciliary processes in large eyes vary in number with the general size of the eye, as in birds—actually, with the size of the cornea, since

it is this which the ciliary body must be thought of as surrounding. They number about 50-100 in carnivores, 60-100 in seals, 90-130 in ungulates and whales, and up to 135 in large-eyed rodents and lagomorphs (hares, beavers). A ciliary web is often present (see Fig. 194b, p. 667); and, in a vestigial condition, it can be made out in man. The tips of the ciliary processes touch the lens in a number of mammals, but they are never fused with it and probably never exert any effective pressure on it in the few mammals which have useful accommodation (primates, squirrels, large carnivores). The mechanics of mammalian accommodation are entirely unlike those of the sauropsidan process, and the difference may be wholly ascribed to the fact that the primitive mammals allowed a 'circumlental space' to be opened up between the ciliary processes and the lens, when they threw away the ossicular ring of their reptilian forebears.

Two chief types of processes are distinguished. The more primitive type is puffy and rugose, like that in monotremes (Fig. 194b, p. 667; *cf.* Fig. 6c, p. 14). This type occurs in all of the lower orders and also in some of the highest—the artiodactyls and perissodactyls, for example. A more specialized type, whose differences from the other have no known functional significance, is the thin, smooth-surfaced, 'knife-blade-like' process seen in most carnivores and pinnipeds and in some primates (Fig. 197a). This type has also been evolved by the higher marsupials (Fig. 196b, p. 673).

The two kinds of ciliary processes are associated with fundamental differences in the organization of the zonule which are perhaps related to the extent of accommodation. In forms with thick processes, some of the zonule fibers arising from the inner surface of the base-plate run for a space along the floors of the valleys between the processes, and others run alongside the faces of the processes. As all these fibers curve out toward the lens, they are quite uniformly distributed both in the aspect of a sagittal section and in the view of the zonule obtained by removing the cornea and iris from a gross specimen. The attachments of the fibers to the periphery of the lens are uniformly distributed both circumferentially and meridionally (Fig. 197d). One cannot speak here of anterior and posterior 'leaves' of the zonule, for there is no canal of Hannover.

The greatest contrast with this situation is seen in the carnivores, as exemplified by the domestic cat, studied by Kahmann. Here the ciliary processes are knife-like, and between every two major ones there is a low secondary process. Zonule fibers arising from the orbiculus segregate into paired bundles as they enter the ciliary valleys, and those in each

bundle form a fan plastered against the face of a major process—one fan against each face. These fibers insert anterior to the lens equator (Fig. 197c). Other fibers arise from the ciliary epithelium alongside the roots of the major processes, and pass along their faces and across the circumlental space to insert posterior to the lens equator. Again there is no canal of Hannover; but the insertions of the fibers are not uniformly scattered around the lens, but are grouped at a number of discrete places—twice the number of the major processes. There is thus an even more free communication (between the bundles) from the anterior chamber to the posterior than in the case of ungulates etc. The anterior surface of the vitreous is plicated where it bulges forward a bit into each ciliary valley, and its pressure against the posterior zonule fibers keeps them bowed; but the anterior fibers take straight courses. The periphery of the lens is scalloped by the discontinuous attachment of the zonule.

The minor processes also have sheets of zonule fibers against their flat surfaces. These arise perpendicularly from the anterior part of the ciliary body and pass to the posterior insertion-zone on the lens. The insertions are in meridians intermediate between those of the major fans (Fig. 197b). All zonule fibers thus lie against ciliary-process surfaces. A frontal section through the ciliary body shows no fiber cross-sections on the floors of the valleys or in the open spaces of the valleys themselves—a great contrast with the ungulates and lower placentals.

According to Kahmann, the primate zonule exhibits still another fundamental plan: Fibers from the greater part of the orbiculus pass only to the anterior lens capsule (forming the anterior leaf), and others from near the posterior ends of the ciliary processes pass only to the posterior capsule, forming a posterior leaf. These two masses of fibers thus cross each other in the coronal zone (the writer is not at all convinced of this). A few of the fibers with orbicular origins insert at the lens equator, and thus travel across the otherwise 'empty' canal of Hannover. Still other fibers, originating far anteriorly, pass to the posterior capsule and thus compare with the 'perpendicular' fans of the cat; but in man there are no regular minor ciliary processes for them to cling to. From these descriptions, it will be seen that where accommodation is considerable (carnivores; and, to a much greater extent, primates*), the zonule fibers which will be most relaxed by the contraction of the ciliary

*The zonules of the squirrels should receive as careful a study as Kahmann has given those of the other strongly-accommodating mammals.

muscle are delegated to the anterior surface of the lens, which exhibits the most elastic deformation. Other fibers, the perpendicular ones, seem to have been oriented favorably to serve as check ligaments, keeping minimal the change in curvature of the posterior surface of the lens.

The lens is nowhere so flat as in man and other diurnal primates. It is perfectly spherical only in seals and in some toothed whales; but it

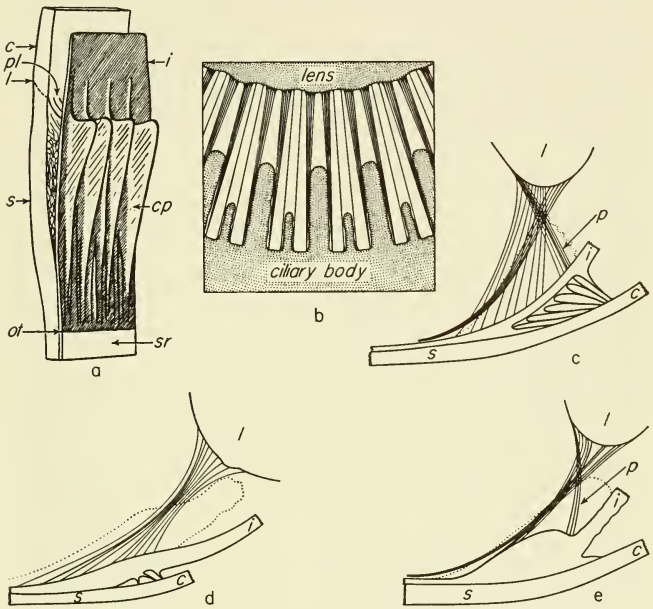

Fig. 197—The ciliary region in placental mammals.

a, portion of anterior segment of a carnivore, *Felis lybica*. Redrawn, modified, from Franz. *c*- cornea; *cp*- ciliary process; *i*- iris; *l*- limbus corneæ; *ol*- ora terminalis retinæ; *pl*- pectinate ligament (three fibers show); *s*- sclera; *sr*- sensory retina.

b, diagrammatic thick frontal section in a carnivore (cat), showing paired bundles of zonule fibers against the faces of the major ciliary processes, and the smaller 'perpendicular' bundles associated with the minor processes. Based upon a photomicrograph of Kahmann.

c, carnivore (cat); d, ungulate (pig); e, primate (man). Combined from figures of Kahmann. Dotted line shows profile of major ciliary process.

c- cornea; *i*- iris; *l*- lens; *p*- perpendicular fans (see text); *s*- sclera.

is very nearly so in many murid rodents and in a few other small-eyed, nocturnal, lower placentals. In carnivores and ungulates it is variously intermediate in shape; and its relative size is always related to the habits of the animal with respect to light (Fig. 71, p. 173).

The Retina—The pigment epithelium usually contains relatively little pigment, which is never migratory (Fig. 20a-c, p. 44). It may contain reflective material and serve as a tapetum lucidum in itself (opossum, Megachiroptera), or in aid of a chorioidal tapetum (dog). Not all fruit-bats have the reflective substance—it is lacking in most species of *Pteropus,* but is abundant in *Pteropus h. condorensis, Hypsignathus, Cynopterus* and *Epomophorus.* It is not apparent whether these differences relate to differences in the strictness of nocturnality of the various genera.

Usually the placentalian retina is described as being, typically, vascularized. Actually, retinal vessels, with capillary branches passing out ordinarily as far as the outer plexiform layer, are numerous only in primates, sciurids, carnivores, and artiodactyls—all, characteristically diurnal or arhythmic (see pp. 654-5). In the primitive ruminant *Tragulus* (the mouse-deer or chevrotain), there are only superficial vessels, like the hyaloid or vitreal vessels of ichthyopsidans and snakes. In most perissodactyls there are no vessels, and in the horse they are restricted to a six-millimeter circle concentric with the disc. There are but few vessels in lagomorphs, associated there with the horizontal band of medullated nerve fibers; and there are few or none in the various rodents outside the Sciuridæ. There are no vessels in the Xenarthra, or in the Chiroptera except for a few superficial capillaries in *Pipistrellus pipistrellus.* Retinal vessels thus seem to have arisen several times, independently, in those placental mammals with the most cones in their retinæ; and certain embryological differences appear to bear out this conclusion. In murids, for example, the few adult retinal vessels are formed directly by the embryonic vasa hyaloidea propria, whereas in primates these atrophy, and the definitive vessels bud out from the central retinal artery and vein in the optic-nerve head.

The lamination and the laminal purity of the placentalian retina are only ordinary, and quite well exemplified by the human retina (Fig. 19, p. 43). Only in the diurnal squirrels and particularly in the prairie-dogs (*Cynomys* spp.), and there only in the dorsal region, does the mammalian retina approach that of the birds in the segregation of inner-

nuclear elements and in the stratification of the inner plexiform layer (*cf.* Fig. 193a, p. 660).

Most placentalian groups have duplex (rod-and-cone) retinæ, but in the lowest orders it seems to be the rule for only rods to be present. The cones are the simplest imaginable—all single, without paraboloids, oil-droplets, or myoid extensibility. There are no cones in the armadillo, possibly none in any edentate. All of the bats have only rods. Among the Lipotyphla, the hedgehogs are pure-rod according to most investigators, though Menner found a few cone-type nuclei. The tree-shrews (*Tupaia et al*) should have many cones; but the shrews have few or none.* There are probably many more pure-rod rodents besides the guinea-pig, and no cones have been reported by modern investigators for any prosimian below the true lemurs†, or by any of the half-dozen investigators who have studied various species of *Aotus*.

The rodents characteristically have great numbers of excessively slender rods, like those of the rodent-like opossums (see Fig. 23f and g, p. 55). Slender rods are also the rule in nocturnal primates and carnivores, and in the fruit-bats. In all such forms the outer nuclear layer is naturally very thick, with up to 16-17 rows of nuclei. The inner nuclear layer in placentals rarely contains more than four or five rows, except in *Tupaia* and in diurnal squirrels, where it may be several times as thick as the outer (*cf.* Fig. 72, p. 177). The ganglion cells usually form but one layer (in which they are often widely separated), except in an area centralis (where any) and in the neighborhood of the primate fovea.

The more slender and numerous the rods, and the fewer the cones, the more likely it is that the rod and cone nuclei will be found markedly differentiated from each other in size, shape, and chromatin distribution (see p. 57).

The cones of most of the placentals which have many of them are much like those of man as a rule (Figs. 19, 22f; pp. 43, 54). In flying-squirrels and ungulates, however, their 'myoid' regions are more or less elongated; and in diurnal squirrels (except prairie-dogs) there appear to be two types of single cones, one bulky proximally and slender distally, the other slender proximally and plumper distally. In prairie-dogs however the cones are all alike, very slender, and not thus pseudostratified.

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*Mlle. Verrier found all the cells alike (and, from her drawings, rods) in *Crocidura mimula;* but in *C. leucodon* and *C. aranea* there are more cones than in mice, according to Schwarz.

†Kolmer claims a few for *Nycticebus tardigradus,* but Detwiler found none in this loris.

Pure-cone retinæ are unknown in mammals outside of the Sciuridæ—none occur even in primates, though some of these (*e.g. Callithrix jacchus, Cercocebus torquatus*) do have many more cones than man. Favorable material of *Tupaia* has never been studied; and there are still other mammals outside the squirrel and monkey tribes which are reputedly strongly diurnal, and whose retinæ would bear investigation: *Ochotona, Dolichotis, Procavia, Cynictis, Suricata, et al.*

The Early History of the Placentalian Eye—The simplicity of the placentalian visual-cell pattern is striking, when one considers that in the lower mammals each of the standard reptilian-avian cell types is easily recognizable. No placental is known to have double cones, or oil-droplets in its single ones.* Obviously the whole sub-class must have been pulled through some sort of ancestral knot-hole: the 'original' placental mammal must have had a way of life which brought about these peculiarities and doomed all of its descendants to exhibit them.

The whole organization of the monotreme eye is, as we have seen, reptilian. If we think of it *as* a reptilian eye, its oddities seem logical consequences of a strong nocturnality of long standing. The reversion of the intra-ocular muscles from a striated to an unstriated condition shows that in the first mammals accommodation became unimportant, and it was never necessary for them to close the pupil quickly—presumably, because they never exposed themselves to bright light. Accommodation is of no value to a strongly nocturnal eye—especially one which, though perhaps relatively large for the animal, is small in absolute dimensions. The discard of the scleral ossicles and the practical discard of the ringwulst of the lens allowed the monotreme eye to become rotund, took the ciliary body out of contact with the lens, and made forever impossible any return to the sauropsidan method of accommodation. Though the persistence of the retinal oil-droplets suggests that the early monotremes may have been sufficiently diurnal to have retained the reptilian eye quite unchanged, the nocturnality which eventually supervened accounts for the condition of the modern monotreme organ.

The marsupial eye, though secondarily arhythmic in capacity in its highest expression (in ground kangaroos), bears the very same stigmata

*Little shrinkage spaces at the distal ends of the cone inner segments have been all too often mistaken for oil-droplets—even by such careful workers as Kolmer. Examination of the retina in its fresh condition, and after fixation with osmic acid, will always demonstrate the presence or absence of real oil-droplets.

of a former universal nocturnality—perhaps even more complete than that of any monotremes, living or dead, since even the scleral cartilage has not been kept. In the opossums, which are the most archaic of living marsupials and hence, so to say, have had the most time in which to get rid of useless structures, some of the single cones have lost their oil-droplets.

The placental mammals must have gone farther in adaptation for dim-light activity, early in their history, than the marsupials have ever done. Their eyes are in fact best understood not by comparison with those of the lower mammals, but by comparison with those of the snakes. The early snakes so completely lost the reptilian assortment of special ocular structures that when the snake eye was rebuilt, upon the return of the snakes to the earth's surface, it ended up as a spherical organ with an entirely fibrous wall, with the lens and ciliary body out of contact (necessitating a new and special method of accommodation), with a wholly new set of visual cells, and (eventually) a yellow lens as a substitute for the ancestral diurnal-lacertilian yellow oil-droplets. To a degree, the placentalian eye incorporates equivalent changes and substitutions. The 'original' placentalian eye was of course not really degenerate like that of a mole or mole-rat, but it did take several steps down the same path which the eye of the incipient snake followed to its bitter end.

Whether the placentals evolved directly from nocturnal marsupials, or turned nocturnal after a derivation from diurnal common ancestors of the modern marsupials and the placentals, we cannot know; nor would the knowledge have much importance. We can be sure that at an early period in placentalian evolution, the only placentals on earth were so thoroughly nocturnal that their eyes had no stiffening structures to keep them from being spherical, had large pupils and large, simple lenses with no trace of a ringwulst and no contact with the ciliary body, had rudimented intra-ocular muscles which were unstriated and did not include a dilatator pupillæ, and had no accommodation whatever.

Now, what was the retina like in these strictly nocturnal, 'bottle-neck' insectivores? Apparently all of the lowest living orders of placental mammals have pure-rod retinæ. But the higher ones have both rods and cones. Do the cones of the higher placentals represent sauropsidan-monotreme-marsupial cones which squeezed through the primitive insectivoran knot-hole, or are they somehow *new*?

Placentalian cones are all alike in certain respects: they are all only single, without paraboloids, and without oil-droplets. These similarities are negative, and really mean that placental cones are cones reduced to their lowest structural terms. Naturally they *would* be alike, even if those of the tree-shrews, the higher primates, the duplex descendants of the pre-creodonts (*i.e.* carnivores, artiodactyls), and the duplex descendants of the Cretaceous pro-ungulates (*i.e.* hyracoids, proboscideans, perissodactyls) all represent independent productions of new cones in erstwhile pure-rod retinæ.

The absence of the paraboloid in placentals is no proof of an identity of placental cones with those of monotremes and marsupials. The latter groups have lost the paraboloid, to be sure; but the cones of placentals would not be expected to have evolved them even if those cones are 'new'. Paraboloids occur only in the cones of groups which have retinal photomechanical changes, and the paraboloid has been claimed to be a reserve of food which furnishes the energy for the activity of the cone myoid. The cones of lampreys and elasmobranchs naturally have never produced them, nor have the cones of snakes, which are certainly 'new' cones.

If the placentalian cone represents the reptilian droplet-bearing single cone, then one can understand its lack of the oil-droplet (*cf.* opossums); but what has become of the reptilian double cone, so stubbornly persisting in even the most strongly nocturnal of the lower mammals except where all cones have been lost (*Tachyglossus*)? Elsewhere above the fishes,* double cones have never been either discarded, or transmuted into rods, without the matching single cones also undergoing discard or transmutation.

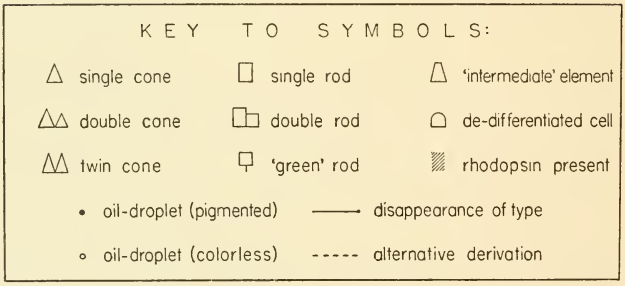
It seems highly significant that the placentalian cone has no consequential capacity for color vision except in the primates, where color vision has evolved within the group (see pp. 518-21). If the duplex placental mammals had had continuously duplex retinæ ever since the placentals originated, then all such mammals, and not the simians alone, should have as complete a color-vision system as that which characterizes the Sauropsida; for, they should have retained that same system—having retained the same cones.

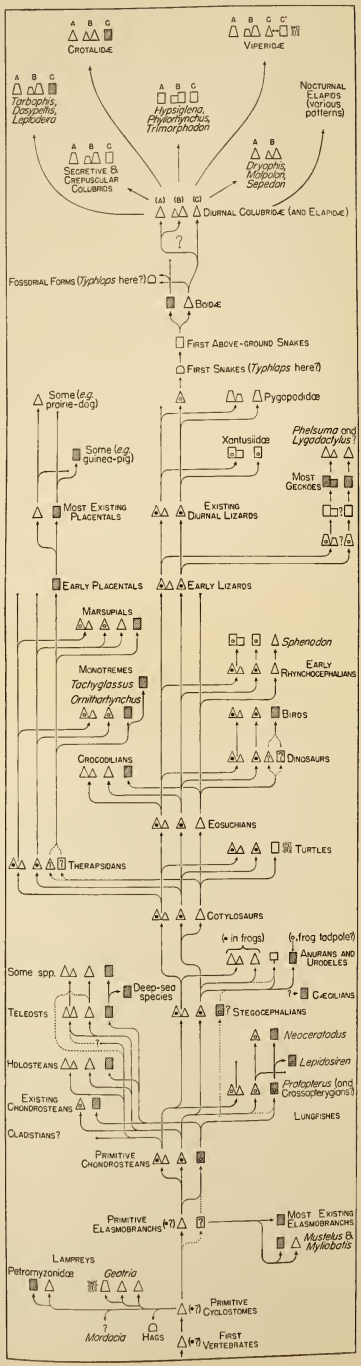
All in all, it seems most probable that at one time the only living placentals had no cones, but only the rods which we see in the lower

*The chondrosteans and *Neoceratodus* have apparently lost ancestral double cones—see Plate I.

mammals, and that subsequent placentals evolved duplex retinæ from pure-rod ones just as the Boidæ or their immediate ancestors had to do (see Plate I). The eye of man, with its pretty-good accommodation, its fovea, its miscellaneous yellow filters, and its capacity for color vision, possesses in substantial degree the physiological capacities of the standard sauropsidan eye as we see it in the lizard or the bird. But it has gained these powers through a lengthy process of re-differentiation, which was carried out largely within the confines of the primate order itself.

Plate I (opposite)—Tentative schema of the evolution of the visual cells in vertebrates. (Pertains to the discussions of the retina in Part III).




A B C
Crotalidae
A B C C'
Viperidae
A B C
Torbophis, Dasypeltis, Lepidodera
A B C
Hypsiglena, Phyllorhynchus, Trimorphodon
Nocturnal Elapids (various patterns)
A B C
Secretive & Crepuscular Colubrids
A B
Dryophis, Malpolon, Sepedon
(a) (B) (C)
Diurnal Colubridae (and Elapidae)
?
Fossorial Forms (Typhlops here?)
Boidae
First Above-ground Snakes
First Snakes (Typhlops here?)
Some (e.g. prairie-dog)
Pygopodidae
Phelsuma and Lygodactylus?
Xantusiidae
Some (e.g. guinea-pig)
Most Geckoes
Most Existing Placentals
Existing Diurnal Lizards
Early Placentals
Early Lizards
Marsupials
Sphenodon
Early Rhynchocephalians
Monotremes
Tachyglassus
Ornithorhynchus
Birds
Crocodilians
Dinosaurs
Eosuchians
Turtles
Therapsidans
Cotylosaurs
(= in frogs)
(= frog tadpole?)
Some spp.
Deep-sea species
Anurans and Urodeles
Teleosts
Gymnophiona
? Stegocephalians
Neoceratodus
Holosteans
Lepidosiren
Protopterus (one Crossopterygian?)
Existing Chondrosteans
Lungfishes
Cladistians?
Primitive Chondrosteans
Primitive Elasmobranchs (=?)
Most Existing Elasmobranchs
Mustelus & Myliobatis
Lampreys
Petromyzonidae
Geotria
Primitive Cyclostomes
?
Mordacia
Hags
First Vertebrates (=?)

P. 59, figure legend, add: *x*- paranuclear body.
P. 72, l. 24, for: pure-cone read: nearly pure-cone.
P. 99, ¶2: Dunlap and Loken (1942) have reported 'cures' of Daltonism.
P. 106, figure legend, l. 9, for: *and* read: and.
P. 109, l. 5, for: amphibians read: fishes and amphibians.
P. 150: Cæcilians have no pigment migration.
P. 184, ll. 32-33: See entry below for p. 568
P. 187: Some owls have deep foveæ.
P. 195, ll. 7-8, for: except in birds read: except in non-strigine birds.
P. 200, for: Petromyzontidæ read: Petromyzonidæ.
P. 201, for: *Ochotona, Castor* read: *Ochotona, Castor, Dolichotus.*
P. 203, l. 8, for: *Anniella* read: *Aniella*; ll. 35-37: *cf.* p. 671.
P. 221, for: *Dryophis* & *Thelotornis* read: *Dryophis, Dryophiops* and
for: *Rhynchops* read: *Rynchops;* [*Thelotornis;*
for: *Indris* read: *Indri.* (Same change, p. 228, l. 14).
P. 223, Fig. 87 legend, for: *Hyperlius* read: *Hyperolius*;
for: *quoyi* read: *gayi.*
P. 236, l. 17, add: *Alburnus bipunctatus, Bliccopsis abramo-rutilus* (*Blicca björkna* × *Rutilus rutilus* hybrid).
P. 237, l. 16, for: *Evermannella* read: *Evermanella.*
P. 240: Note p. 585, last ¶.
P. 254, l. 33, and p. 270, l. 6, for: Macrochiroptera read: Megachiroptera.
P. 266, figure legend, ll. 6-7, for: only the ventral one read: none.
P. 270, figure legend, for: *punctatus* read: *punctatum.*
P. 273: Urodeles have no pupillary nodules.
P. 312, l. 9, for: Elliott read: Elliot.
P. 386, l. 8, for: *Galeorhinidæ* read: Galeorhinidæ;
l. 14, for: Raja read: *Raja.*
P. 409, figure legend, for: Pettit read: Petit.
P. 434, figure legend, for: Schneider and von Orelli read: Schneider-von Orelli.
P. 450: Delete *Aniella* (see footnote, p. 625). Under 'significance', for: fossorial read: fossorial or nocturnal. Under 'lids fused' and opposite 'vestige', add: Lizards: diurnal geckoes.
P. 452, l. 25, for: retractor bulbi muscle read: rectus muscles.
P. 494, l. 18, for: colorvision read: color vision.
P. 506, l. 2, for: Orbelli read: Orbéli.
P. 511, l. 26, for: Abbot read: Abbott.
P. 518, ll. 33-34: See entry below for p. 568.
P. 527, ll. 8, 9, 14, and p. 535, l. 18, for: Babak read: Babák.
P. 556, l. 22, for: homologous read: homoiologous.
P. 561, figure legend, for: in *Myliobatus aquila* read: in *Lamna cornubica* and *Myliobatis aquila.* (See next entry).
P. 568, last ¶: Rochon-Duvigneaud (1939) figures distinct cones (and rods) for *Lamna cornubica.*
P. 589, *re* Cladistians: According to Rochon-Duvigneaud (1939), *Polypterus congicus* has only rods, the inner segments of which are plump and cone-like (*i.e.*, as in dipnoans? with oil-droplets?); and the horizontal-cell processes are thin (*cf.* pp. 591, 598).
P. 608, sub-index: Delete entry for p. 72.
P. 663, col. 2, l. 9, for: reraction read: refraction.
P. 676, l. 10, delete: taguans or;
l. 22: comma at end of line belongs at end of l. 20.
P. 686, l. 2, for: *Callithrix* read: *Hapale.*

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NOTE: The list of titles which follows is but a tiny portion of the whole literature of the eye. Its items have therefore been selected carefully. I have tried to include the sources of borrowed illustrations, and the more important works of all authors specifically mentioned in the text—in some instances citing only the author's later contributions, the bibliographies of which will provide leads to the earlier work of that author and others. I have included a number of books, compilations, and monographs whose long lists of literature will give the beginner a good start in compiling his own card-catalogue of those phases of the subject which interest him most. Certain of these major works (some of them now obsolete, but definitive in their time) should perhaps be the first to be consulted by the new investigator of the vertebrate eye, and these have been starred (*). The more important of my own papers are also listed, and I have ventured to star a couple of those whose bibliographies contain a number of important references which have been omitted here.

I have included a few non-ophthalmological items (and where their titles are not self-explanatory, I have annotated them); but I have made no attempt to list all of the sources of my zoölogical and ecological information, for to cite any reasonable number of pertinent works would serve only to give them undue emphasis. Some zoölogical writings are mines of information; but many a book must be read through for the sake of gaining a single ophthalmological fact. The beginning investigator of the vertebrate eye must read omnivorously in the natural-history field, and is well advised to maintain a correspondence with the curators of the nearest research museum of vertebrate natural history.

The reader will note that the non-clinical literature of the eye is sadly scattered—there have been only two periodicals, both short-lived, which were entirely devoted to comparative ophthalmology. These were the *Zeitschrift für vergleichende Augenheilkunde* (7 vols., 1882-93) and the *Archiv für vergleichende Ophthalmologie* (4 vols., 1910-14). Each of these contains many valuable abstracts as well as original contributions. The student should also make the acquaintance of the *Journal of the Optical Society of America,* the extinct *American Journal of Physiological Optics* (7 vols., 1920-6), and the *Untersuchungen aus dem Physiologischen Institut des Universität Heidelberg* (4 vols., 1877-82). Aside from the latter, which contains practically all of Kühne's work on rhodopsin, the only general journals which have been heavily comparative-ophthalmological are the *Jenaische Zeitschrift für Naturwissenschaft* and the *Zeitschrift für vergleichende Physiologie.* The student simply must keep constant watch for new contributions in all of the morphological, physiological, and ophthalmological journals.

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NOTE: The list of names which follows is offered the beginning investigator as a check-list of workers, most of them still living and active, who have been particularly productive in the field of this book in recent years or are likely to be especially productive in the future. These are names to watch for in perusing past and future issues of the bibliographic periodicals. Not all of these investigators are wholly 'trustworthy'—two or three are decidedly not, but are included here because they are too prolific to be ignored.

In the accumulation of titles and abstracts of the current non-clinical literature and that of recent past years, the student will find the following publications helpful: *American Journal of Ophthalmology* (abstracts); *Anatomischer Anzeiger* (international bibliography); *Archives of Ophthalmology* (abstracts); *Biological Abstracts; British Journal of Ophthalmology* (abstracts, transactions); *Chemical Abstracts; Physiological Abstracts* (and the Annual Review of Physiology); *Psychological Abstracts; Quarterly Cumulative Index Medicus* (titles with subject classification); *Scientiae Naturalis Bibliographia* (titles); *Special Reports of the Committee upon the Physiology of Vision, (British) Medical Research Council* (each an extensive research or review, with a comprehensive bibliography); *Zentralblatt für die gesamte Ophthalmologie und ihre Grenzgebiete* (abstracts); and *Zoological Record* (titles with subject classification).

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Allen, Frank
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Bartley, S. Howard
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Birukow, Georg
Bishop, George H.
von Bonin, Gerhardt
Brecher, G. A.
Breder, Charles M., Jr.
von Buddenbrock, W.
Bull, H. O.
Butcher, Earl O.
Chard, Ray D.
Chase, Aurin M.
Clark, W. E. LeGros
Cobb, Percy W.
Cogan, David G.
Crozier, William J.
Curtis, Brian
Detwiler, Samuel R.
Franz, Viktor
Fry, Glenn A.
Glücksmann, A.
Graham, Clarence H.
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Halstead, Ward C.
Hamilton, W. F.
Hartline, Haldan K.
Hecht, Selig
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Mann, Ida C.
Marshall, Wade H.
Matthews, Samuel A.
Meader, Ralph G.
Menner, Erich
Merker, E.
Moore, George A.
Munsterhjelm, A.
Murr, Erich
O'Leary, James L.
O'Day, Kevin J.
Osborn, Clinton M.
Pitt, F. H. G.
Polyak, Stephen
Roaf, H. E.
Rochon-Duvigneaud, André
Riggs, Lorrin A.
Sachs, Erich
Scharrer, E.
Schmidt, W. J.
Skolnick, Alec
Smith, G. Elliot
Stroër, W. F. H.
von Studnitz, Gotthilft
Sumner, Francis B.
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ABBREVIATIONS AND SYMBOLS

Å, Å.u.	=	Ångstrom unit = 0.1 mμ
ca.	=	*circa* = approximately
cf.	=	*confer* = compare
e.g.	=	*exempli gratia* = for example
et al	=	*et alii* = and others
i.e.	=	*id est* = that is
λ	=	lambda = symbol for wavelength
m.	=	meter = 39.38 inches
μ	=	mu = micron = .001 mm.
mm.	=	millimeter = .001 m.
mμ	=	millimicron = .001 μ
π	=	pi = 3.1416
φ	=	phi = symbol for diameter
q.v.	=	*quod vide* = which see
sp.	=	species
spp.	=	species (plural)
s.s.	=	*sensu strictu* = in the strict sense
vs	=	*versus* = as against
v.i.	=	*vide infra* = see below
v.s.	=	*vide supra* = see above
>	=	greater than
<	=	less than
√	=	square root of
:	=	to (ratio sign)

INDEX AND GLOSSARY

NOTE: Page numbers in **boldface** indicate illustrations (and may also refer to textual matter pertaining to the item). A starred (*) page number indicates that the item will be found defined or characterized on that page. Other terms (not clearly defined in the text, or likely to be unfamiliar to the reader) will be found defined or characterized here as regards the senses in which they have been used in the text. The arrangement of sub-items is alphabetical except in certain instances where a taxonomic arrangement seemed likely to prove more convenient.

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absorption of: the reception of light in a material and its conversion into radiation of longer wavelengths (usually 'heat'—infra-red 'light'); absorption and fluorescence are essentially the same phenomenon; *cf.* fluorescence, below.
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fluorescence of: the reception of short-wave (usually ultra-violet) light in a material and its re-radiation at longer (usually visible) wave-lengths; differs from 'absorption' only as to the portion of the grand spectrum involved; 375, 488-489
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interference of: a phenomenon occurring in extremely thin films of reflective material, wherein light rays reflected from the top and bottom surfaces of the film are variously out of phase, resulting in cancellation of some wavelengths and reinforcement of others, so that the reflected light is colored though the incident light be white and the film devoid of differentially-absorbing (colored) substances; 231, 526, 543
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limitans: external limiting membrane of [retina, *q.v.*
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littoral: living in the water over shores and beaches
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mutations: unpredictable, marked, hereditary peculiarities which appear in progeny, but whose basis is in accidental changes in the germ-plasm of the parental generation; *e.g.*, the occurrence of an albino in a normal strain or family
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octave: a span of frequencies or wavelengths such that the highest is exactly twice the lowest
oculorotatory muscles: those which turn the eyeball, as apart from other extra-ocular, oculomotor muscles such as retractors, levators, nictitans-operators, etc.; see muscles
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osculant: said of a species or group related to two others which it directly connects—a living link as opposed to a 'missing' (*i.e.*, extinct) one
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pars cæca retinæ: the thin, blind, anterior continuation of the retina, extending from ora terminalis to pupil
pars ciliaris retinæ: the portion of the pars cæca which covers the inner surface of the ciliary body
pars iridica retinæ: the portion of the pars cæca which covers the posterior surface of the iris
pars optica retinæ: the seeing portion of the retina (*i.e.,* the portion provided with visual cells), posterior to the ora terminalis
pars plana: the flat portion of the ciliary body; orbiculus ciliaris
pars plicata: the anterior portion of the ciliary body, which bears the ciliary processes; corona ciliaris
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great blue: *Prionace, q.v.*
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luminous: *Etmopterus, q.v.*
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uvea, uveal tract: chorioid + ciliary body + iris, *qq.v.*

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vascular, vascularized: supplied with blood vessels
ventrad: toward the ventral side (of an
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